

Transactions of the
**Royal Society of South
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**DECORIBATULA GEN. NOV. FROM SINGAPORE, WITH NOTES ON
ALLIED RETZCULOPPIA (ACARIDA: CRYPTOSTIGMATA:
ORIBATULIDAE) FROM TROPICAL AUSTRALIA.**

BY DAVID C. LEE & CAROLYN M. BIRCHBY*

Summary

Decoribatula pustulata gen. nov., sp. nov. on an orchid from Singapore, intercepted at Adelaide Airport, is described. It is similar to *Reticuloppia reticulata* Balogh & Mahunka, 1966 from rainforest litter in Queensland, the description of which is extended. Both mites are unusual in having a deficient chaetotaxy on femora I and II.

KEY WORDS: Acarida, Oribatulidae, *Decoribatula pustulata*, new genus, new species, *Reticuloppia reticulata* Balogh & Mahunka, Singapore, Queensland, leg chaetotaxy.

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Summary

LEE, D. C. & BIRCHBY, C. M. (1989) *Decoribatula* gen. nov. from Singapore, with notes on allied *Reticuloppi* (Acarida: Cryptostigmata: Oribatulidae) from tropical Australia. *Trans. R. Soc. S. Aust.* 113 (2), 1-5, 31 May, 1989.

Decoribatula pustulata gen. nov., sp. nov. on an orchid from Singapore, intercepted at Adelaide Airport, is described. It is similar to *Reticuloppi reticulata* Balogh & Mahunka, 1966 from rainforest litter in Queensland, the description of which is extended. Both mites are unusual in having a deficient chaetotaxy on femora I and II.

KEY WORDS: Acarida, Oribatulidae, *Decoribatula pustulata*, new genus, new species. *Reticuloppi reticulata* Balogh & Mahunka, Singapore, Queensland, leg chaetotaxy.

Introduction

The mites considered here have been studied because of their relevance to an ongoing study of sarcoptiform mites of South Australian soils, sampled from nine florally diverse sites. An introduction to relevant work on the advanced oribate mites (*Plano fissuræ*), with comments on the Oripodoidea, which include the Oribatulidae, is provided by Lee (1987). These mites and a group of seven species of *Oribatula*-like mites from the South Australian study are atypical within the Oripodoidea in that they have a deficient chaetotaxy on femora I and II. Oripodoid leg chaetotaxy will be discussed more fully when the South Australian species are described (Lee & Birchby in preparation). The chaetotaxy for femur I and II on oripodoid mites is 0 anterior; 2 dorsal/2 ventral, 1 posterior setae (0,2/2,1). In the deficient chaetotaxy one or two setae are missing, resulting in one of three chaetotaxies as follows: 0,2/2,0; 0,2/1,0; 0,2/1,1. The *Oribatula*-like S. Aust. mites differ superficially in having only short or medium length hysteronotal setae and they were collected from only the arid, semiarid or mallee sites; whilst the two species considered here have long hysteronotal setae and are from moist, tropical sites.

The notation and methods of measurements follow Lee (1981) with modifications made by Lee (1987). Measurements are in micrometers (μm). The type of the new species is deposited in the South Australian Museum, Adelaide (SAMA) whilst the type of *Reticuloppi reticulata* is deposited in to the Hungarian National Museum, Budapest.

***Reticuloppi* Balogh & Mahunka**

Reticuloppi Balogh & Mahunka, 1966; p. 564.

Type-species: *Reticuloppi reticulata* Balogh & Mahunka, 1966.

Diagnosis: Oribatulinae. Hysteronotum with 14 pairs (5J, 6Z, 3S) of long setae. Lamella absent. Hysteronotal lenticulus present near dorsosejugal furrow. Integument of hysteronotum with extensive reticulate sculpturing and cerotegument forming a thick, columnar refractile exudate. Femora I and II with deficient chaetotaxy, lacking posterior setae: I - 0,2/2,0; II - 0,2/1,0. Legs slim and long, with leg IV longest (leg III is lost). Pretarsal claws short (central claw II less than 0.33 x length of tarsus II) and lateral claws much slimmer than central claw (depth less than 0.5 x depth of central claw II).

Remarks: *Reticuloppi* is based on a single female, grouped in the Oribatulinae, and distinguished by the hysteronotum having a large number of long setae and reticulate sculpturing around a lenticulus (Balogh & Balogh 1984). In addition, the proteronotum lacks ridges, having only a weak sublamella, and the leg chaetotaxy is deficient in a way that is unique amongst established oripodoid species.

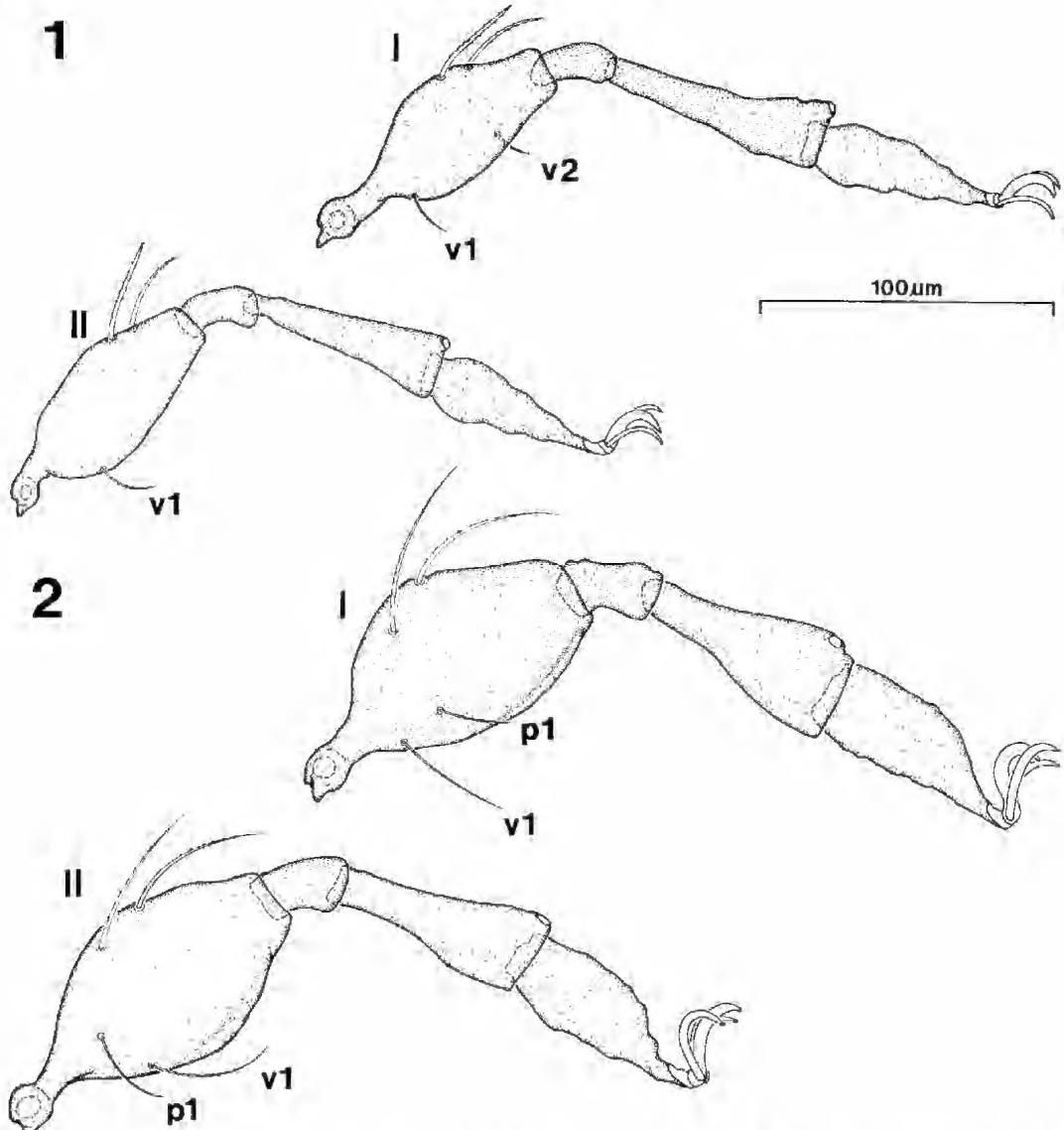
***Reticuloppi reticulata* Balogh & Mahunka**

FIG. 1

Reticuloppi reticulata Balogh & Mahunka, 1966; p. 564.

Female: Idiosomal length, 475 (470 in original description). Leg lengths (femur-tarsus); I - 270, II - 254, III - 7, IV - 311. Tibial maximum heights: I - 25.5, II - 20.5, III - 7, IV - 18. Yellow brown colour. Thick (Maximum depth equal to distance between setae z1-/2), whitish, columnar refractile

* South Australian Museum, North Terrace, Adelaide, S. Aust. 5000



Figs 1-2: Posterior aspects of femur-pretarsus of right legs I and II, all setae on femora illustrated, *p* = posterior, *v* = ventral. 1, *Reticuloppiia reticulata* Balogh & Mahunka. 2, *Decoribatula pustulata* sp. nov.

cerotegument on proteronotum anterior to *J2*, thickest lateral to seta *z1*; also covering hysteronotum except around lenticulus and near pleural margins, with thick patches posterolateral to seta *S1*, lateral to *S5* and between setae *J6-J6*.

Proteronotum with faint costate sublamella. Sensory seta (*z2*) with long stalk (length = $\times 3$ caput). Margin of bothridium raised into turret-like structure, height subequal to length of *z2* caput. Seta *z2* short (0.5 \times or less distance between setae *j2-z1*), fine, smooth, without cilia. Hysteronotum with fine reticulate sculpturing under columnar exudate. Five multiporose foramina, foramen *F3* divided in *F3a* and *F3b*. Hysteronotal seta *S1*

confirmed similar to and nearly as long as *Z1*. Podosternal chaetotaxy: *3I*, *1II*, *3III*, *3IV*, with all third rank setae as long as *II3* (illustrated in the wrong position by Balogh & Mahunka 1966, fig. 15) and *I3* on pedotectum I, *III3* posterior to pedotectum II (as for *Decoribatula pustulosa* sp. nov., Fig. 4), *IV3* on discidium. Seta *Sa1* shorter than *Sa2* and *Sa3*. Opisthosternum with foveolate sculpturing. Four subcylindrical eggs, exochorion smooth, 80 \times 230 (mean). Legs long (mean femur-tarsus: 59% of soma) and slim (mean maximum tibial height: 27% of mean length).

Material examined: Holotype female, rainforest litter, Mt Spec (18°57'S, 146°11'E), Townsville, Qld,

19.iii.1965, J. Balogh. Some appendages lost, no femur-tarsus III on either side.

Remarks: The further description here of *Reticuloppiella reticulata* adds to or corrects the original description, with a few important confirmations. Reference to the relative dimensions of the legs is distorted by legs III being lost (usually a short, slim leg amongst the opipodoids).

Decoribatula gen. nov.

Type species: *Decoribatula pustulata* sp. nov.

Diagnosis: Oribatulinae. Hysteronotum with 14 pairs (5J, 6Z, 3S) of mainly long setae (S1 is short). Lamella with only costate anterior part present, not reaching bothridium to seta z2. Smooth, paler mid-dorsal anterior area on hysteronotum, but not clearly delineated as lenticulus. Integument of hysteronotum with extensive foveolate sculpturing, cerotegument inconspicuous. Femora I and II with deficient chaetotaxy, but with posterior setae: I = 0.2/1.1; II = 0.2/1.1. Legs of medium girth and long, with leg IV longest. Pretarsal claws long (central claw II more than 0.33 x length of tarsus II) and lateral claws only slightly slimmer than central claw (depth more than 0.5 x depth of central claw II).

Remarks: *Decoribatula* is based on a single male. It is similar to *Reticuloppiella* in having a deficient femoral chaetotaxy, long hysteronotal setae, a divided anterior hysteronotal foramen (F3a, F3b) and a turret-like bothridium to z2. It particularly differs, in having a lamella, a different type of cerotegument, a different type of setal loss on femora I and II and unusually large pretarsal claws. On the basis of this it is considered to be a sister-group to *Reticuloppiella* but different enough to be regarded as a separate genus.

Decoribatula pustulata sp. nov.

FIGS 2-4

Male: Idiosomal length, 527. Leg lengths (femur-tarsus): I = 298, II = 280, III = 285, IV = 323. Tibial maximum heights: I = 36, II = 31, III = 23, IV = 23. Red brown colour. Inconspicuous (depth less than diameter of hysteronotal setal bases) cerotegument, concentrated in round or oval pustules on hysteronotum.

Proteronotum with partial costate lamella, superficially inconspicuous but backed by retractile internal apodeme, not reaching back to turret-like bothridium to seta z2. Two multiporose

foramina (F1, F2d) recognisable dorsally. Central setae (j1, j2, z1) with 3 or 4 files of cilia, j2 longest. Sensory seta (z2) with caput and exposed stalk subequal in length. Seta s2 short (0.6 x or less distance j2-z1), fine, smooth, without cilia.

Hysteronotum with smooth central triangulate area from anterior margin to level with seta J3, but no clearly delineated pale lenticulus. Five multiporose foramina (F3a, F3b, F4, F5, F6) each backed by a disc-shaped chamber in integument. Hysteronotal setae smooth, S1 short, subequal to s2, whilst J5 and S5 very long with whip-like end.

Podosternum with reticulate sculpturing. Subpodal ridge in three parts, pedotectum II and discidium large, extending laterally beyond level of pedotectum I. Lateral setae (especially II/3) longer than central setae. Opisthosternum with three setae (JZg4, JZg5, Sg) represented only by bases on both sides and assumed broken off. Seta Sa1 longer than Sa2 and Sa3. Shield dark, centrally horizontal and punctate with curving upwards, smooth marginal strip.

Legs long (mean femur-tarsus: 56% of soma), with leg I second longest, and of medium girth (mean maximum tibial height: 35% of mean length). Ventral flange on trochantera III and IV. Femora with ventral incrustation.

Material examined: Holotype male (SAMA N1988474), on orchid from Singapore, intercepted at Adelaide International Airport, 13.iv. 1987, Greg Baker (S. Aust. Department of Agriculture).

Remarks: The male of *D. pustulata* is described, although opipodoid species are usually based on females, because it is unlikely that more material will be collected and this species is important to the classification of S. Aust. mites being studied (Lee & Birchby in preparation). There is a lack of sexual dimorphism amongst opipodoid character states that are considered important in distinguishing species. The female is likely to be bigger and have the thickening around the genital orifice separated from the ventroscutal apodeme. Its relationships are considered under the remarks on *Decoribatula*.

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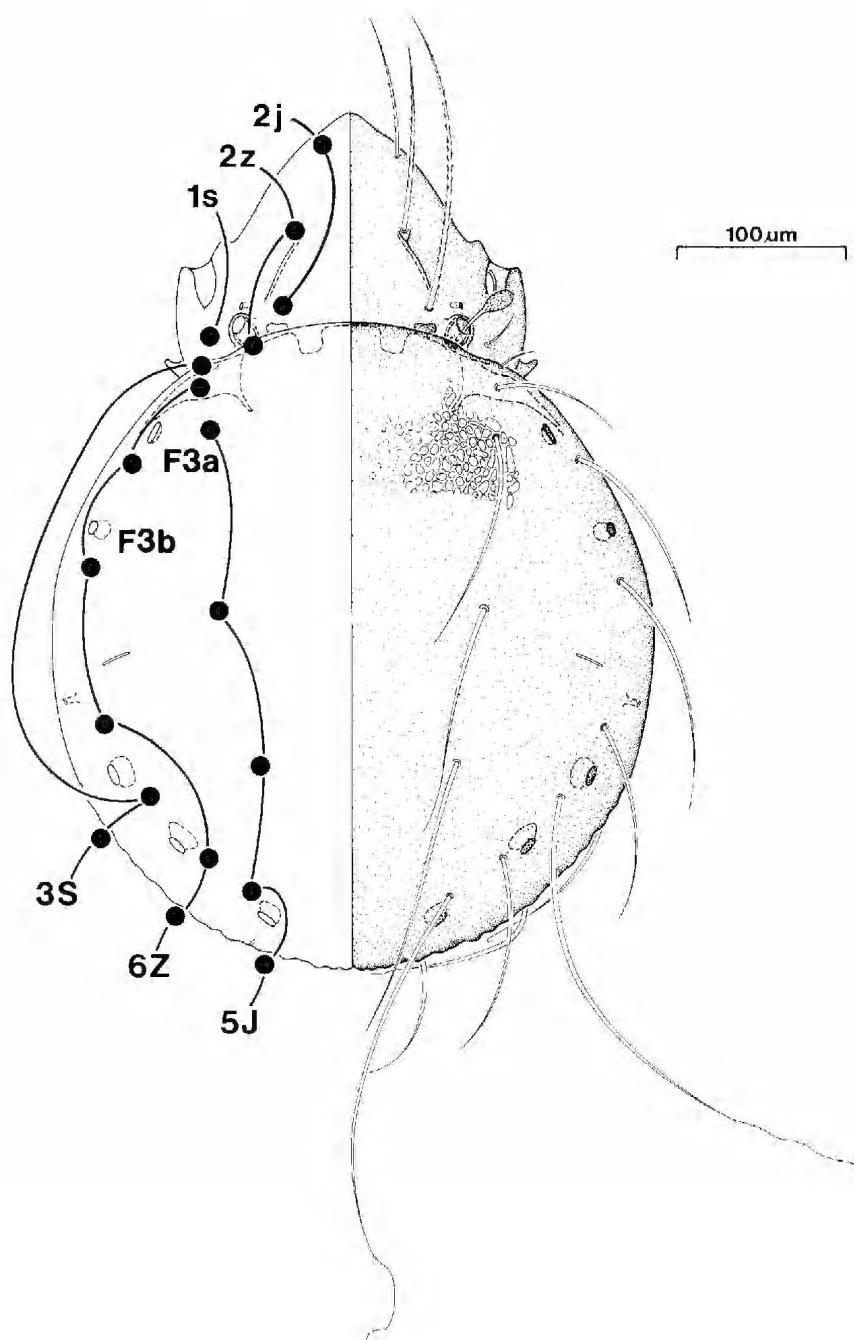


Fig. 3: *Decoribatula pustulata* sp. nov., notum of soma.

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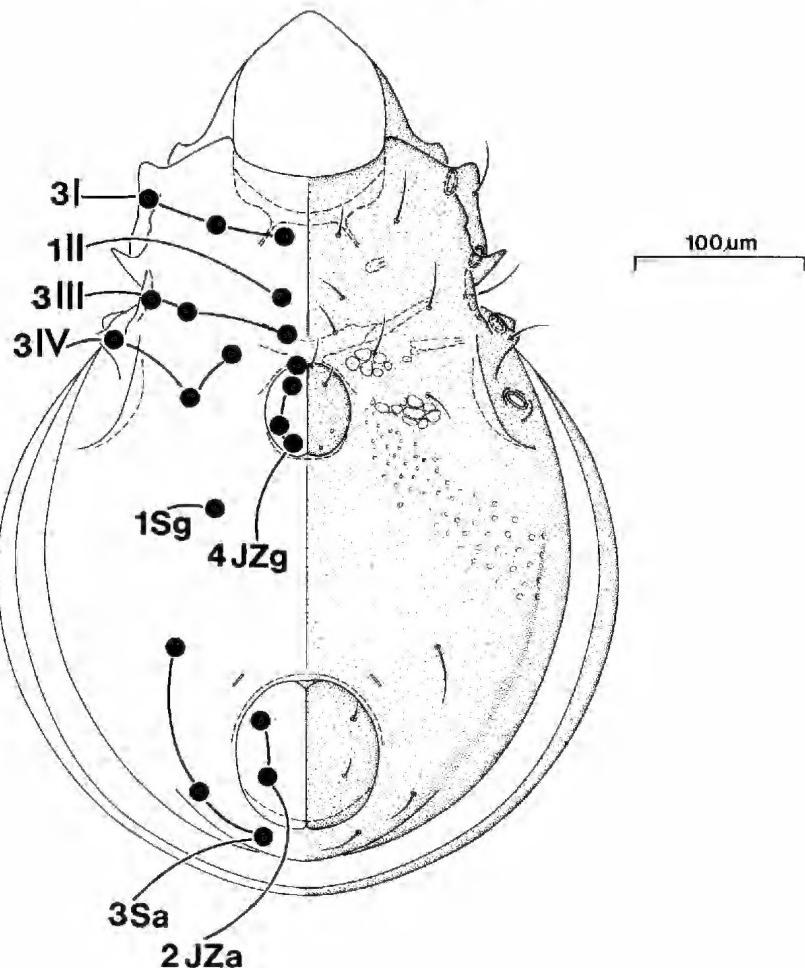


Fig. 4: *Decoribatula pustulata* sp. nov., sternum of soma.

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A NEW GENUS OF HUNTSMAN SPIDER (HETEROPODIDAE:ARANEAE) FROM SOUTH EASTERN AUSTRALIA

BY DAVID HIRST*

Summary

A new heteropodine genus, *Keilira*, gen. nov. and two new species, *K. sparsornaculata* sp. nov. and *K. sokoli* sp. nov. are described from South Australia and Victoria respectively. *Keilira* differs from other Australian genera in labium shape and the relatively short, thick embolus of the male. The arrangement of cheliceral teeth is similar to that of *Heteropoda* Latreille, 1804, but the general appearance resembles Australian species attributed to *Olios* Walckenaer, 1837, here considered as belonging in *Neosparassus* Hogg, 1903.

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Summary

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A new heteropodine genus, *Keilira*, gen. nov. and two new species, *K. sparsomaculata* sp. nov. and *K. sokuli* sp. nov. are described from South Australia and Victoria respectively. *Keilira* differs from other Australian genera in labium shape and the relatively short, thick embolus of the male. The arrangement of cheliceral teeth is similar to that of *Heteropoda* Latreille, 1804, but the general appearance resembles Australian species attributed to *Olios* Walckenaer, 1837, here considered as belonging in *Neosparassus* Hogg, 1903.

KEY WORDS: Araneae, Heteropodidae; *Keilira* gen. nov., new taxa.

Introduction

This paper forms the first part of a taxonomic study on the Australian Heteropodidae. A new heteropodine genus is defined for undescribed species previously mis-identified as *Neosparassus* (subfamily Deleninae Hogg, 1903), which they resemble in general colouring and shape. *Neosparassus* will be discussed fully later (Hirst in prep.), but it may be mentioned here that despite its re-validation by Jarvi (1974) all relevant species have been referred to *Olios* in subsequent literature.

Subfamilies of the Heteropodidae are poorly defined. Some useful characters of the Heteropodinae Keyserling, 1880 are referred to here in associating the new genus with that subfamily. Similarly, characters of the Deleninae are mentioned in comparing *Neosparassus* with *Olios*. Although limits of that subfamily are uncertain, it is retained here as separate from the Eusparassinae (Jarvi 1972) on the basis of genitalic structure.

Materials and Methods

All measurements are in millimetres, made with an eyepiece graticule. Eye diameters, interspaces and MOQ measurements are expressed as relative to the diameter of an AME. Drawings were done with the aid of a camera lucida on a Wild microscope. All abbreviations are standard for the Araneae. Bilateral variability of leg spine counts are indicated in parenthesis. Types are deposited in the South Australian Museum, Adelaide (SAMA), and the Australian Museum, Sydney (AM).

Keilira gen. nov.

Diagnosis: Labium twice as broad as long. Male embolus short, thick relatively straight with a curved

tip. Female with small fossa and hood-like anterior margin.

Definition: Carapace raised, flattish or convex in profile, highest in the fovea region, sloping gently to clypeus. Foveal groove weak or indistinct. Eyes subequal. Anterior eye row slightly recurved. Posterior eye row straight to slightly recurved. Clypeus half width of an AME or slightly less. Cheliceral fang groove with three teeth on promargin, three or four teeth on retromargin and one or more median rows of minute, pointed teeth. Labium at least twice as broad as long. Sternum barely longer than broad or equal, slightly convex. Legs 2143. Anterior legs with four ventral pairs of spines on tibia, without an extreme distal pair. Reduced prolateral leg spination, patellae without prolateral spines. Female palp tarsal claw with four small teeth. Female genitalia with paired uncoiled spermathecae. Small fossa with weakly sclerotized hood-like anterior margin. Male embolus short, thick, relatively straight with a curved tip. Palpal tibia with a small prodorsal distal extension and a triangular spur rising from a retrolateral apophysis.

Type-species: *Keilira sparsomaculata* sp. nov.

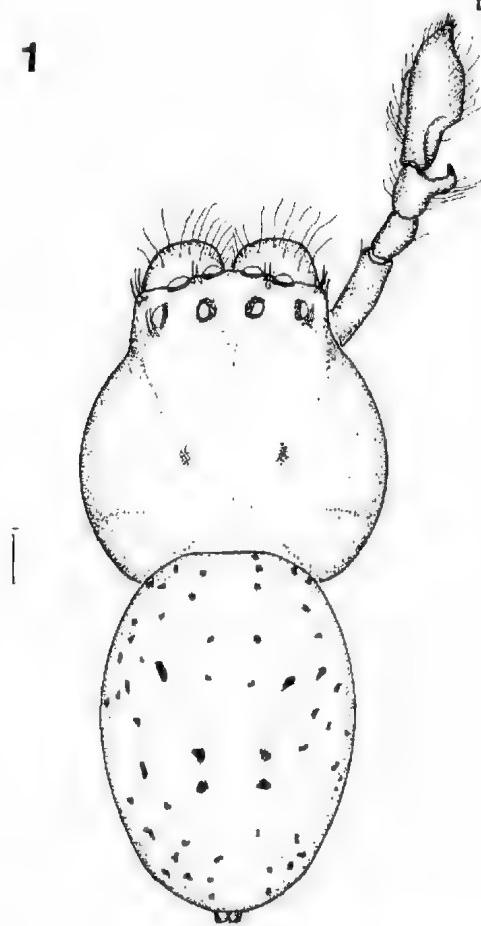
Comments

Although resembling *Neosparassus* in body shape and coloration, the presence of a distal prodorsal extension on the tibia of the male palp and three teeth on the promargin of the chelicerae followed by one or more rows of median teeth, places the genus close to *Heteropoda* and *Panderces* L. Koch, 1875, the Australian representatives of the Heteropodinae. *Neosparassus* and other genera of the Deleninae lack median teeth and a well defined extension on the male palp tibia.

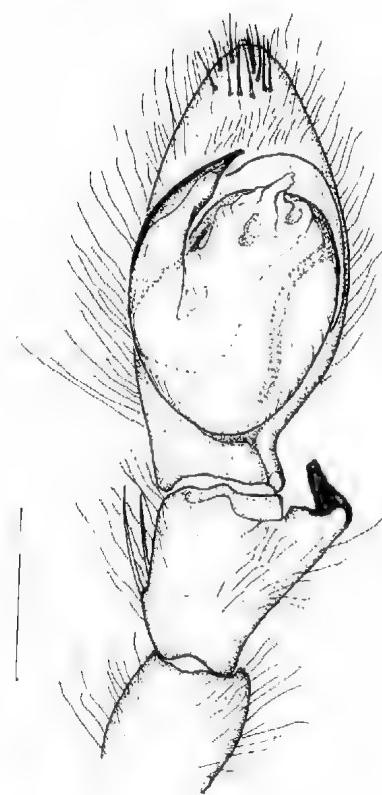
The retromarginal teeth of *Keilira* differ from those of *Heteropoda* and *Panderces* in that both the latter have four long teeth which are evenly sized and close together with a small space between the two middle teeth. In *Keilira* greater spacing occurs

*South Australian Museum, North Terrace, Adelaide, S.Aust. 5000.

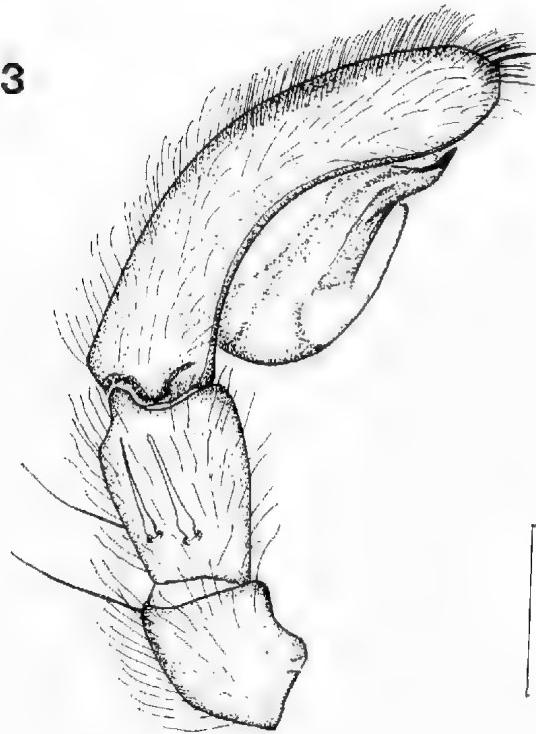
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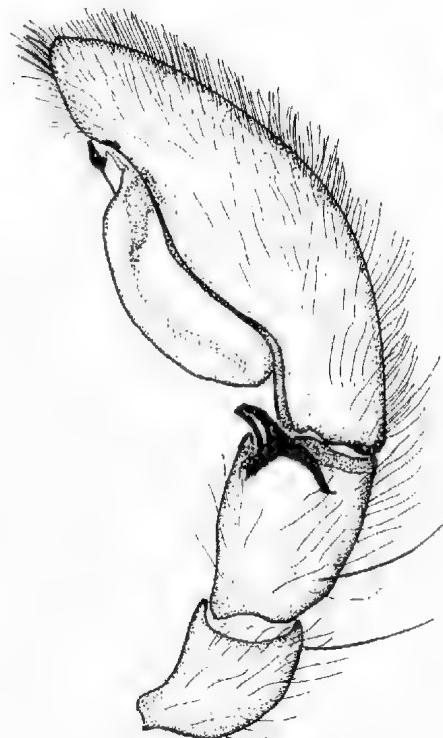
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between the middle and distal teeth (Fig. 8). This placement remains unchanged when a fourth tooth is present, this being minute and found at the proximal end of the row (Fig. 12).

The teeth of the female palp tarsal claws of *Heteropoda* and *Pandercetes* are elongated and curved, as long or longer than the curved claw tip, and comb-like. This condition is approached in at least one other Australian heteropodid, *Olios kennensis* Hogg, 1914, the correct generic status of which is unknown as no mature specimens have been seen. The elongated teeth on the palpal claw are not found in *Keilira*, but as all other Australian genera normally possess at least five teeth, it is unusual in having four.

Keilira and *Pandercetes* have four ventral spine pairs on anterior tibiae but lack a distal pair. While four ventral spine pairs are found in *Heteropoda*, one pair is shorter and positioned distally near the articulation with the metatarsi. This character was used by Kaston (1980) to distinguish *Heteropoda* from *Olios*, the latter having two pairs and lacking an extreme distal pair. *Neosparassus* and most other Deleninae genera have three pairs with the distal pair near the articulation. The exceptions are some species of *Pediopa* Simon, 1880 and juvenile specimens of at least *Isopeda* L. Koch, 1875 and *Neosparassus* (juveniles of other genera have not been examined). There, the distal spine is represented as a bristle barely distinguishable from those adjacent on the tibia margin.

Keilira is similar to *Heteropoda* in carapace profile and in having leg I shorter than leg II (*Pandercetes* has a concave carapace profile and leg I longer than leg II), but differs in eye position and relative size of the anterior median eyes. The male bulb, in the unexpanded state, resembles that of *Pandercetes* and, to a lesser extent, *Heteropoda*. *Keilira* lacks the long tapering embolus typical of other Australian heteropodid genera, having a relatively straight, short, thick embolus which tapers at the tip to a blunt point. For much of its length the embolus runs adjacent to the bulb. In *Pandercetes* and *Heteropoda* the embolus is well clear of the bulb for its entire length.

It can be concluded that *Keilira* is referable to the Heteropodinae, yet is distinct from *Heteropoda* and *Pandercetes*. However, it is known that Heteropodinae genera of uncertain status occur in Queensland with five or six ventral spine pairs on anterior tibia. These are not congeneric with *Keilira* (unpubl. data) but appear to be closely related and may prove to be a sister group.

Keilira contains the smallest known Australian heteropodids. Its representation by a handful of specimens from the south-eastern parts of both South Australia and Victoria extends the known range of the Australian Heteropodinae. Little is known of their biology but they appear to have similar habits to *Neosparassus* (Main 1976). Several specimens of *Keilira sparsomaculata* were collected whilst foraging at night on low flowering shrubs (*Leptospermum juniperinum* Sm.), which were attracting abundant insects, a habitat three species of *Neosparassus* have also been found sharing. One juvenile specimen of *Keilira* was found in litter at the base of shrubs during the day.

Etymology: The generic name *Keilira* is derived from Keilira Station, 31 km N.E. of Kingston, S.E. South Australia.

Keilira sparsomaculata sp. nov.

FIGS 1-10

Holotype: SAMA N19875, ♂, 13 km N. of Keilira Station, 36° 37'S, 140° 11'E, S. Aust., Feb. 1974, D. Hirst.

Allotype: SAMA N19876, ♀, same data as holotype.

Paratypes: SAMA N19877, ♀, same data as holotype; SAMA N19878, ♀, Cortina Station, Coorong, 36° 20'S, 139° 46'E, S. Aust. 20.I.1968, A.W. Forbes.

Other material examined: SAMA N19872, Juvenile, Cortina Station, same data as above; SAMA N19873, Juvenile, Kendall Station, Coorong, S. Aust., Mar. 1968, A.W. Forbes; SAMA N19874, Juvenile, Aldinga Scrub, S. Aust., 16. ix. 1987, D. Hirst.

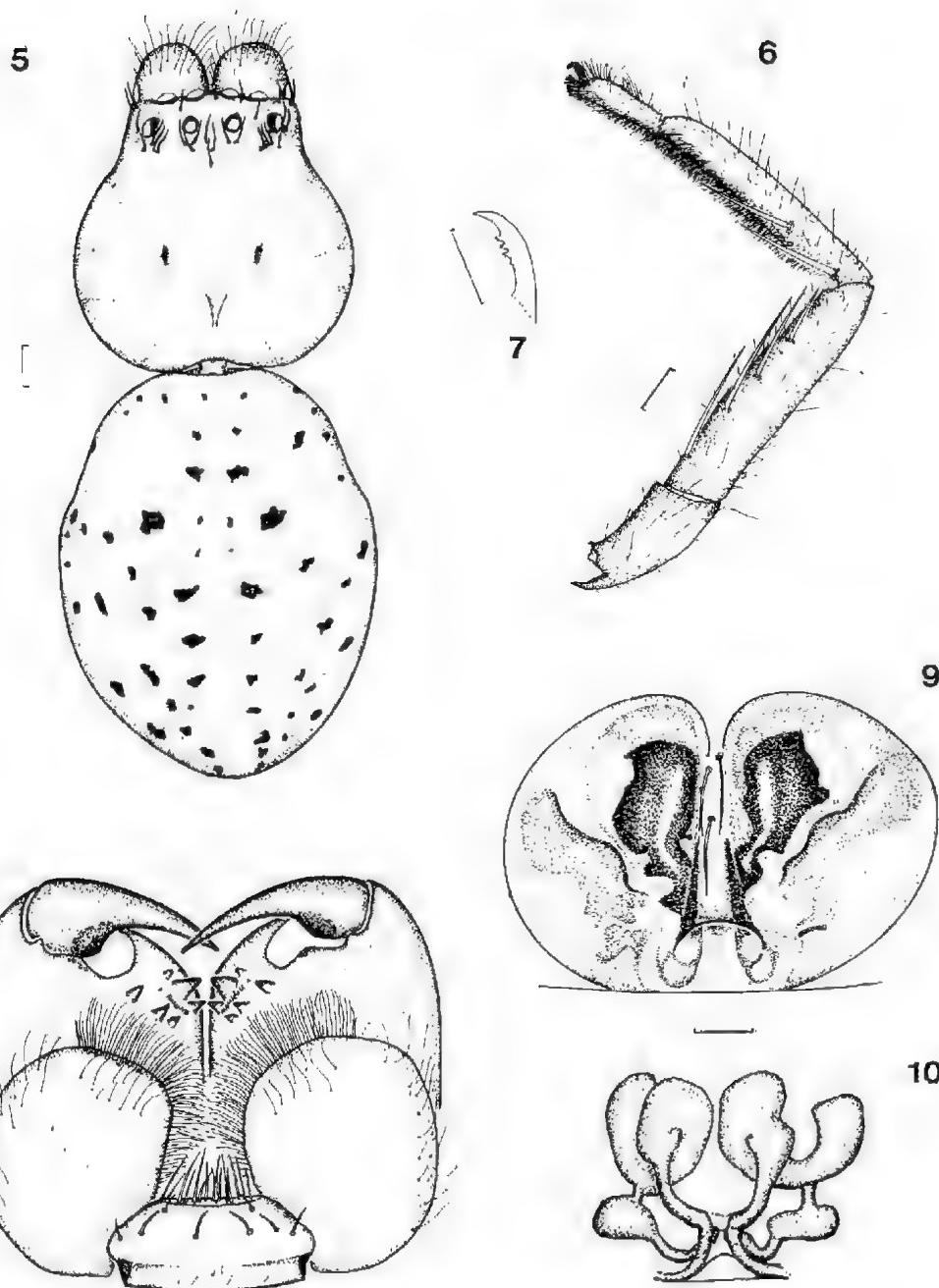
Description of holotype (Figs 1-4) Carapace length 2.90, width 2.85. Abdomen length 3.40, width 2.20.

Colour in alcohol: Yellow-brown carapace with pair of median black, short linear markings with adjacent spots, anterior of fovea. Caput with darker suffusion in ocular region, eyes with black rims. Chelicerae reddish-yellow. Sternum yellowish. Legs: anterior pairs yellow-orange, posterior pairs yellow, palps yellow. Abdomen creamish-white with small scattered spots of black pigment, fewer ventrally.

Carapace: Convex, highest between II coxae sloping gradually to clypeus, steeply to posterior. Fovea indistinct, marked by darker pigment. Setae sparse, short (ca 0.2), moderately long (ca 0.4) bristles around ocular region, few on caput between eyes and fovea and along lower margin of clypeus.

Eyes: In two rows, from above anterior row slightly recurved, posterior row straight. AME

Figs. 1-4. *Keilira sparsomaculata* gen. et sp. nov. Holotype male: 1 body and right palp, dorsal; 2-4 Left palp. 2 ventral; 3 prolateral; 4 retrolateral. Scale lines = 0.5mm.



Figs. 5–10. *Keilira sparsomaculata* gen. et sp. nov. Allotype female, 5–8; 6 right leg I, prolateral; 7 tarsal claw; 8 chelicerae, maxillae and labium. Paratype female (SAMA NI9878), 9–10: 9 epigyne; 10 vulva, ventral. Scale lines: Figs 5–6, 8 = 0.5mm; figs 7, 9–10 = 0.1mm.

diameter 0.20. AME : ALE : PME : PLE = 1 : 1 : 0.9 : 0.9. Interspaces: AME - AME 0.8; AME - ALE 0.5; PME - PME 1.55; PME - PLE 1.55; AME - PME 1.1; ALE - PLE 1. MOQ: anterior width : posterior width : length = 2.75 : 3.4 : 2.65.

Chelicerae: Length 1.20, width 1.69, geniculate, almost glabrous, setae long (ca. 0.6), shorter on retromargins. Three rows of teeth on fang groove: three teeth on promargin, middle tooth largest, three teeth on retromargin, middle and distal teeth about equal, median row of about eleven minute pointed teeth, placed posterior to middle tooth of promargin row. **Labium:** Length 0.30, width 0.70, emarginate postero-laterally, six short setae in recurved row across anterior half with one near anterior margin midway towards each lateral edge. Longer setae on anterior margin, few setae on posterior half. **Maxillae:** Length 0.75, width 0.63, slightly converging, setae long. **Sternum:** Length 1.25, width 1.22, slightly convex, setae long.

Legs: (Table I). Scopula sparse. Spines: Leg I, fe d2 p2 r3 (2 on right se), ti r1 v8, mt v4; Leg II, fe d2 p3 r1, ti v8, mt v4; Leg III, fe d2 p3, ti v4, mt p2 v4; Leg IV, fe d2 p1, ti p1 v3, mt p2 v4; Palp, fe d2 p1 all distal, ti p2. **Claws:** Teeth small with about 6 on proclaw, 4-5 on retroclaw.

Abdomen: Setae of short to moderate length. **Spinnerets:** ALS basal segment 0.30, apical segment 0.08, PLS 0.20, 0.08.

Palps: (Figs 2-4) Tibia terrolaterally with apophysis carrying a short triangular blunt-tipped spur. Embolus thick, short, straight for the most part along prolateral side of cymbium, then curved inwards with a short blunt tip.

Description of allotype (Figs 5-10): As in holotype but for the following: Carapace length 3.51, width 3.50. Abdomen length 5.10, width 3.80. Colour in alcohol: Abdomen creamish with larger black spots.

Eyes: AME diameter 0.24. AME : ALE : PME : PLE = 1 : 1.04 : 0.92 : 0.92. Interspaces: AME - AME 0.67; AME - ALE 0.5; PME - PME 1.3; PME - PLE 1.5; AME - PME 1; ALE - PLE 0.92. MOQ: Anterior width: posterior width: length = 2.8 : 3.2 : 2.6.

Chelicerae: Length 1.60, width 2.10. **Labium:** Length 0.36, width 0.80. **Maxillae:** Length 0.94, width 0.71. **Sternum:** Length 1.80, width 1.80.

Legs: (Table I). Spines: Leg I, fe (3 on right), ti r2; Leg II, fe (2 on right); Leg IV, fe p2, mt p3 r1.

Spinnerets: ALS basal segment 0.36, apical segment 0.08; PLS 0.30, 0.10.

Genitalia: Epigynum a low mound, highest posteriorly, small fossa with weakly sclerotised hood-like anterior margin (Fig. 9). Vulva paired, copulatory openings inside hood, spermatheca

leading to a curved receptaculum shortly joined to a smaller receptaculum (Fig. 10).

Etymology: The specific name refers to the widely scattered spots on the abdomen.

Kelira sokoli sp. nov.

FIGS 11-15

Holotype: AM KS19141, ♂, Holey Plains State Park, 38° 13' S, 146° 51' E, Vict., 29. iii. 1980, A. Sokol.

Description of Holotype: Similar to *K. sparsomaculata* except as follows: Carapace length 3.44, width 3.22. Abdomen length 3.90, width 2.20.

Colour in alcohol: With blackish markings laterally on carapace. Abdomen with numerous spots.

Carapace: Raised but flattish above, highest in foveal region, fovea distinct.

Eyes: Both rows slightly recurved, AME diameter 0.20. AME : ALE : PME : PLE = 1 : 0.9 : 0.8 : 0.9. Interspaces: AME - AME 1; AME - ALE 0.9 ; PME - PME 1.7 ; PME - PLE 1.6 ; AME - PME 0.9 ; ALE - PLE 0.8. MOQ: Anterior width : posterior width : length = 3.0 : 3.4 : 2.3.

Chelicerae: Length 1.44, width 1.72. Retromargin with four teeth, irregular median rows of 8-13 minute teeth arranged in triangular area with apex pointing distally. **Labium:** Length 0.36, width 0.76. Short setae on posterior half. **Sternum:** Length 1.76, width 1.70.

Legs: (Table 2). Spines: Leg I fe dl p2 r3, ti r2 v8, mt p1 r2 v4; Leg II, fe dl p2 r2, ti r1 v8, mt p2 r2 v4; Leg III, fe d2 p2, ti p2 r2 v4, mt p2 r2 v4; Leg IV, fe dl p1 ti v4, mt p1 r3 (2 on right) v4; Palp, fe d2 p1, all distal, ti dl p2 r5.

Palp: Tegulum positioned more basally in cymbium than in *K. sparsomaculata* and enlarged retrolaterally at proximal end. Embolus extending further in prolateral side; distal half straighter. Tibial spur longer and more upright on larger apophysis.

Etymology: The species is named after the collector, A. Sokol.

Remarks

Known only from the holotype, *K. sokoli* is separated from *K. sparsomaculata* by the flatter carapace, four retrolateral teeth on the fang margin, several irregular rows of median teeth and abdomen with more numerous spots. Its habits are not known.

Acknowledgments

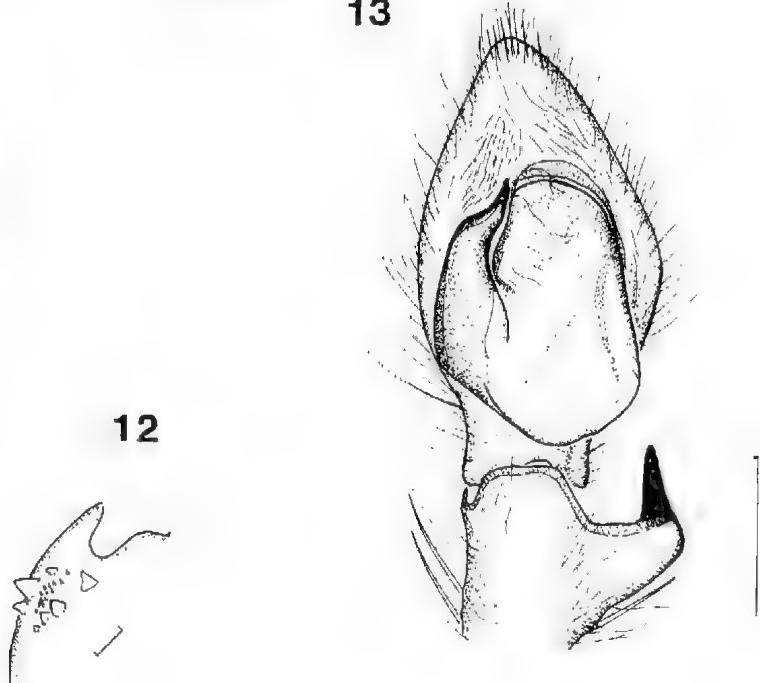
The completion of this paper was supported by an Australian Biological Resources Study grant. Special thanks go to Dr D. C. Lee for his helpful comments on manuscript preparation. Also to Dr M. Gray and C. Horsemian (AM) for the loan of material and assistance.

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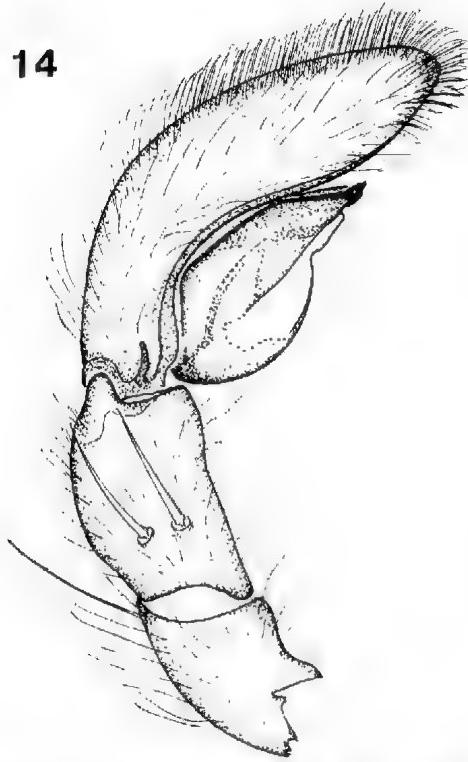
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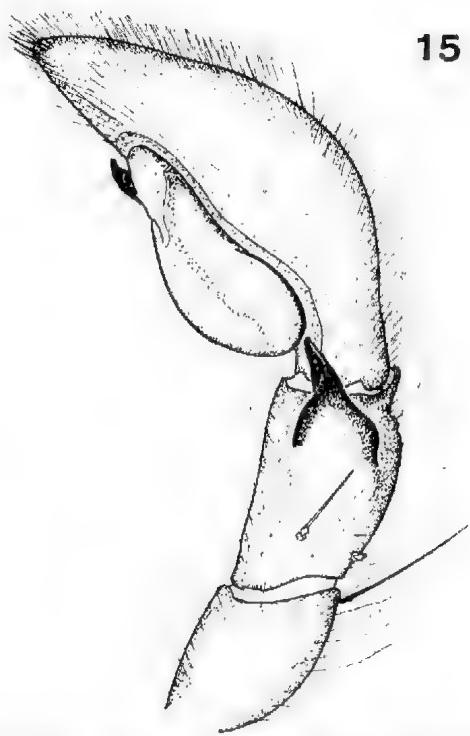
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Figs 11-15. *Keilira sokoli* gen. et sp. nov. Holotype male: 11 Abdomen, dorsal; 12 cheliceral teeth, left retrolateral; 13-15 left palp; 13 ventral; 14 prolateral; 15 retrolateral. Scale lines: Figs 11, 13 - 15 = 0.5mm; Fig. 12 = 0.1mm.

TABLE I. Leg measurements of *Keilira sparsomaculata* gen. et sp. nov. values for holotype male with allotype female in parentheses.

Lég	Femur	Patella	Tibia	Metatarsus	Tarsus	Total
I	2.85 (3.32)	1.55 (1.84)	2.58 (2.82)	2.50 (2.92)	0.90 (1.12)	10.38 (12.02)
II	3.21 (3.68)	1.69 (2.00)	2.92 (3.16)	2.92 (3.16)	0.98 (1.24)	11.72 (13.24)
III	2.32 (2.56)	1.12 (1.38)	1.70 (1.96)	1.69 (1.81)	0.80 (0.95)	7.63 (8.86)
IV	2.45 (2.84)	1.15 (1.36)	2.00 (2.24)	2.15 (2.40)	0.88 (1.00)	8.63 (9.84)
Palp	1.00 (1.00)	0.52 (0.74)	0.49 (0.80)	-	1.50 (1.52)	3.51 (4.06)

TABLE 2. Leg measurements of *Keilira sokoli* gen. et sp. nov. of holotype male.

Leg	Femur	Patella	Tibia	Metatarsus	Tarsus	Total
I	3.48	1.83	3.30	3.20	1.04	12.85
II	4.20	1.95	3.84	3.58	1.14	14.71
III	2.88	1.38	2.18	2.04	0.84	9.32
IV	3.34	1.30	2.52	2.64	0.92	10.72
Palp	1.10	0.66	0.67	-	1.50	3.93

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**A NEW SPECIES OF LECHRZODUS (ANURA: LEPTODACTYLIDAE)
FROM THE TERTIARY OF QUEENSLAND, WITH A REDEFINITION OF
THE ILIAL CHARACTERISTICS OF THE GENUS**

BY MICHAEL J. TYLER

Summary

A large collection of frog ilia from the Tertiary site of Riversleigh Station in northwestern Queensland, includes 190 specimens of *Lechriodus intergerivus* sp. nov. The new species is described, compared with the four extant congeners, and shown to be the smallest member of the genus. A revised definition of the ilium of *Lechriodus* is provided, and the significance of the find as a link between the geographically isolated extant species is discussed. The rainforest habitat preferences of all extant species suggest a similar environment at Riversleigh Station in the Late Oligocene to Mid-Miocene.

KEY WORDS: *Lechriodus*, ilia, Leptodactylidae, Tertiary, Queensland.

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TYLER, M. J. (1989) A new species of *Lechriodus* (Anura: Leptodactylidae) from the Tertiary of Queensland, with a redefinition of the ilial characteristics of the genus. *Trans. R. Soc. S. Aust.* 113, 15–21, 31 May, 1989.

A large collection of frog ilia from the Tertiary site of Riversleigh Station in northwestern Queensland, includes 190 specimens of *Lechriodus intergerivus* sp. nov. The new species is described, compared with the four extant congeners, and shown to be the smallest member of the genus. A revised definition of the ilium of *Lechriodus* is provided, and the significance of the find as a link between the geographically isolated extant species is discussed. The rainforest habitat preferences of all extant species suggest a similar environment at Riversleigh Station in the Late Oligocene to Mid-Miocene.

KEY WORDS: *Lechriodus*, ilia, Leptodactylidae, Tertiary, Queensland.

Introduction

Lechriodus Boulenger comprises a group of ground-dwelling leptodactylid frogs confined to the Australian Geographical Region. In addition to the morphological attributes that support its recognition, it is unique in the nature of its distribution; of the five leptodactylid genera that have been reported to occur both in Australia and New Guinea, it is the only one which is represented by more species in New Guinea than in Australia (Zweifel 1972).

McDonald & Miller (1982) clarified the geographic distribution of *Lechriodus* in Australia, demonstrated that a previous record from north Queensland was in error, and confirmed that there is a major disjunction between the Australian and New Guinea populations. Thus, whereas other shared genera occupy the Cape York Peninsula of north Queensland (Tyler 1972), *Lechriodus* does not, and in Australia it is confined to the eastern seaboard along the Great Dividing Range between Ourimbah, N.S.W., and Brisbane, Qld. All that can be interpreted about such allopatry is that at some time in the past *Lechriodus* must have occurred in the intermediate area.

Here I report a new species of *Lechriodus* from the Tertiary. The material comes from Riversleigh Station in northwest Queensland, which is intermediate between the distribution of the extant species. The finding is significant for several reasons: it constitutes the link in the distribution of the extant species; it is the first record of fossil *Lechriodus*, and it is the first occasion on which an Australian frog fossil has been reported from a site that is beyond the modern geographic range of its genus.

Material and Methods

The material is deposited in museums and other collections abbreviated in the text as follows: Australian Museum, Sydney — AM; Department of Zoology, University of Adelaide — AUZ; Queensland Museum, Brisbane — QM; South Australian Museum, Adelaide — SAM, and American Museum of Natural History, New York — AMNH. Letters following the abbreviations are departmental identifications.

Comparative studies were based on the osteological collections of the Department of Zoology, University of Adelaide, supplemented by skeletal material of New Guinea taxa borrowed from the American Museum of Natural History.

Osteological nomenclature follows Tyler (1976). The following measurements were taken with dial callipers: ilial length — measured from the superior extremity of the dorsal acetabular expansion to the distal end of the shaft; dorsal acetabular expansion to ventral acetabular expansion (DAE-VAE) measured as the distance between their extremities, and acetabular fossa diameter measured at the proximal, external edge of the peripheral acetabular rim.



Fig. 1. Orientation of ilium to horizontal plane during preparation of descriptions.

All measurements and descriptive features are derived from the lateral surface. Expressions of relative extent of features are obtained with the ilium positioned in such a way that the proximal edge of the bone is maintained at 45° to the horizontal (Fig. 1). Concepts of relative size of

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component features to one another are perceived with regard to their proportional size in other anuran taxa.

Scanning electron micrographs were taken on an ETEC Autoscan SEM at 20 Kv.

Systematics

Family: Leptodactylidae Werner, 1896.

Sub-family: Limnodynastinae Lynch, 1971

Genus: *Lechriodus* Boulenger, 1882

The definition of the generic characteristics of the ilium by Tyler (1976) was based solely on *L. melanopyga* (Doria). Now that representatives of all extant species and the fossil species have become available, the definition requires modification and expansion:

Ilium shaft slightly to moderately curved, bearing large, fanlike dorsal crest extending along at least three-quarters its length. Maximum depth of dorsal crest approximately one-third from proximal end. Crest concave to varying extents proximally, flattened distally.

Acetabular fossa diameter varies with size of individual from which it is derived; proportionally larger in larger species. Acetabular fossa bordered by rim in large species; rim confined to inferior half in smaller species. Location of dorsal margin of acetabulum ranges from base of ilial shaft to midway up shaft.

Pre-acetabular zone narrow, meeting inferior border of ilial shaft in gentle curvature, commonly forming quadrant. Ventral acetabular expansion moderately developed, commonly truncate inferiorly.

Dorsal prominence small, extending superiorly above superior margin of ilium, or not. Dorsal prominence moderately to well developed, oval and horizontal or vertical.

Dorsal acetabular expansion acutely angled, its superior margin on a level with or above the maximum extent of the dorsal crest.

Lechriodus intergerivus sp. nov.

FIG. 2

Holotype: QM F16614. An almost entire left ilium collected at C.S. Site, Riversleigh Station, Queensland.

Description of holotype: Ilium shaft slightly curved and bears enlarged, fanlike dorsal crest whose maximum depth is at position approximately one-third from proximal end of shaft. Proximal one-half of crest concave on lateral surface, progressively becoming less pronounced distally. Distal half of crest flat.

Acetabular fossa small, deep and with prominent rim bounding inferior half. Dorsal margin of acetabular fossa situated slightly superior to inferior margin of ilial shaft.



Fig. 2. S.E.M. of *Lechriodus intergerivus* (SAM P29771). A left ilium, but image reversed to aid comparison with Fig. 3.

Pre-acetabular zone evenly rounded with narrow separation from acetabular fossa. Ventral acetabular expansion poorly developed and incomplete inferiorly.

Dorsal acetabular expansion narrow but well developed superiorly, extending to position approximately on a level with maximum extent of superior margin of ilial crest.

Dorsal prominence poorly developed and scarcely detectable; in profile visible as slight superior extension upon dorsal margin of ilium. Dorsal protuberance ovoid, lateral, well developed and projecting laterally. Anterior margin of dorsal prominence extends to position slightly anterior to anterior margin of acetabulum.

Length of ilium 13.6 mm; DAE-VAE 3.7 mm; acetabular fossa maximum diameter 1.4 mm.

Paratypes: Henk's Hollow Site: SAM P29742; Two Trees Site: AM F76951-52, AMNH 25351-53; Last Minute Site: SAM P29764-65; Gag Site: AM F76957, AMNH 25355-58, SAM P27968; Upper Site: AM F76953-54, 76958, AMNH 25354, QM F16640-50, 17036-39, SAM P29734, 29743-44, 29757-62; C.S. Site: AM F76955-56, 76959, AMNH 25359-60, QM F16615-18, 16674, 17031-32, SAM P29746-50; Wayne's Wok Site: AM F76960, QM F16636-39, 17034-35, 17040-47, SAM P29756, 29760-67; Oulasite Site: SAM P27929, 29751-55; R.S.O. Site: QM F16619-35, 17033, SAM P29735-41, 29745, 29771 (subject of S.E.M.).

Variation: The complete ilia range in length from 5.3 mm to 14.4 mm. A paratype is shown in Fig. 2. There is minimal difference in overall shape, and variation is largely confined to the position of the dorsal prominence in relation to the acetabulum. Thus some specimens agree with the holotype in having the anterior margin of the prominence on a level with the anterior margin of the acetabulum, in others the anterior half of the prominence may project beyond the acetabulum.

The extent and degree of the curvature of the dorsal crest varies in terms of its elevation, proximal limit and medial protrusion.

Referred specimens: Small portions of an additional 79 specimens are sufficiently complete to permit identification, but so fragmentary that they do not contribute to an understanding of the nature or variability of the species. For those reasons they are considered here "referred specimens" rather than paratypes. All of the referred specimens are lodged in the Queensland Museum: Henk's Hollow Site: F16652; Two Trees Site: F16688-89; Last Minute Site: F16673, 16675, 16678-79, 16685; Gag Site: F16651, F16676-77, 16680-83, 16686-87, 16700-01; Upper Site: F16658-59, 16665-72, 17050-53; C.S. Site: F16660-64, 16684, 16690, 17048; R.S.O. Site:

F16653-57, 16691-99, 17049; Wayne's Wok Site: F16702-14, 17054-63.

Comparison with other species: Ilia of all extant species have been examined: *L. fletcheri* (Boulenger) (AUZ 8 uncat.); *L. melanopyga* (Doria) (AMNH 81223, AUZ 2 uncat.); *L. aganoposis* Zweifel (AMNH 74646), *L. platiceps* Parker (AMNH 74178). Representatives are shown in Fig. 3.

The comparisons assume that the sample size of *L. intergerivus* is sufficient to reflect with reasonable confidence the size of ilia attained by the species. With that assumption it is relevant to note that the absolute sizes of the ilia examined of each of the adults of New Guinea species is substantially larger than any of the *L. intergerivus*.

The relationship between ilial length and snout to vent length of extant species is almost linear. Thus given ilial length alone it is possible to extrapolate snout to vent length. The longest ilium of *L. intergerivus* is 14.4 mm. The corresponding snout to vent length derived from the closely linear relationship of congeners is approximately 37.5 mm (Fig. 4). This, the apparent maximum is less than two-thirds of the size of the smallest adult *L. aganoposis* and *L. platiceps*, and is slightly below the range of *L. melanopyga* and *L. fletcheri* (Table 1). Clearly *L. intergerivus* is the smallest member of the genus.

As indicated by the generic definition, the ilium in this genus is conservative and interspecific variation is not pronounced. For that reason I am reluctant to ascribe differences in ilial characters greater significance than they may merit. However, given the data on size, the integrity of *L. intergerivus* is not in question.

Stratigraphy and lithology: The assumed stratigraphic sequence of the sites at Riversleigh is that followed in the list of paratypes. Of the sites named to date those containing *L. intergerivus* form an almost uninterrupted sequence. One of the fossil bearing sediments is described by Hand (1985) as fine-grained arenaceous freshwater limestones, and possibly a facies within the Carl Creek Limestone. The ages of the sediments containing *L. intergerivus* are currently understood to be between Late Oligocene and Middle Miocene (M. Archer pers. comn.).

Etymology: Latin for "placed between", so alluding to the geographic position of the fossil population between those of the extant species.

Phylogeny: Zweifel's (1972) proposed phylogenetic relationships is reproduced here as Fig. 5. Given the geographic location of *L. intergerivus* (Fig. 6), the age of the Riversleigh Station deposits, and the fact that the lower estimation of age is contemporaneous with the emergence and subsequent uplift of most



Fig. 3. Ilia of extant species with or without ischium and pubis; A. *Lechriodus fletcheri* (AUZ uncat.); B. *L. melanopyga* (AMNH 81223); c. *L. platyceps* (AMNH 74178); D. *L. aganoposis* (AMNH 74646).

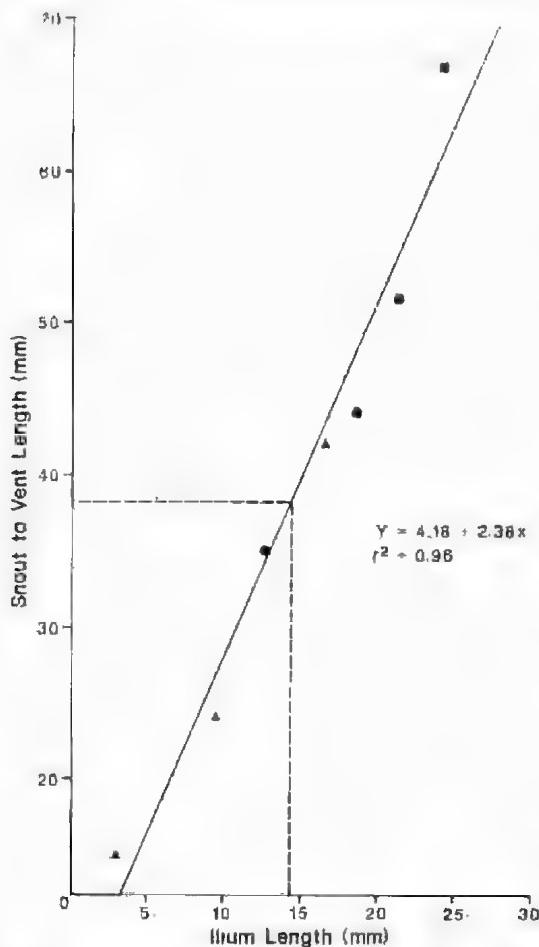


Fig. 4. Length of ilia of *Lechriodus* species plotted against snout to vent length. Assumed snout to vent length of fossil species indicated by broken lines. t -value for slope 10.891, $p < .001$. For $x = 14$, $y = 37.51$ (95% confidence limits = 33.75–41.25). Square = *L. platyceps*; circles = *L. melanopyga*; triangles = *L. fletcheri*.

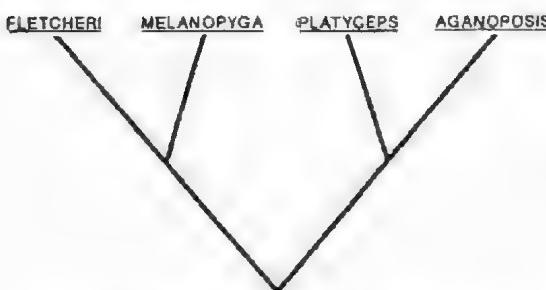


Fig. 5. Phylogenetic relationships of extant species of *Lechriodus* as postulated by Zweifel (1972).

of New Guinea, *L. intergerivus* is a candidate as the ancestral stock from which the extant species evolved.

With the existence of *L. intergerivus*, Zweifel's phenetic scheme would require two invasions into New Guinea: one deriving *L. melanopyga* from an intermediate ancestor that also gave rise to *L. fletcheri*, and the other leading to *L. platyceps* and *L. aganopsis*. A slightly simpler scenario would derive *L. fletcheri* directly from *L. intergerivus*, with a second stock giving rise to the three New Guinea species. Further systematic studies are required to test the validity of that option.

Discussion

The fossil frog fauna of Australia includes 22 species and nine genera from 10 sites of Quaternary or Tertiary age (Tyler 1989). Riversleigh Station appears likely to be the richest fossil frog site yet discovered, in terms of the number and diversity of species. This trend is common to other vertebrate classes, and Archer, Hand & Godthelp (1988) state that more than 200 new species have been recovered there. The frog fauna will increase the total.

Amongst the frog material from Riversleigh Station now available, *L. intergerivus* is the predominant species. Of 379 ilia now known from the site 190 (50%) represent that species.

Extant *Lechriodus* are predominantly inhabitants of temperate and sub-tropical rainforest and, in the absence of any data to the contrary, it can be inferred that the habitat of *L. intergerivus* would have been rainforest. A second point relevant to interpreting the mid-Miocene environment is the fact that a high proportion of the ilia of other frog species found in Riversleigh Station deposits are from small creatures. Because frogs lose water readily through the skin, the body mass/surface area ratio is such that small frogs are particularly vulnerable to dehydration. In consequence they are predominant only in areas which are moist throughout the year. In communities of frogs in Australia high frequency of small frogs occurs only in areas of high and seasonally reliable rainfall, such as the extreme southwest of Western Australia and the northern periphery of Arnhem Land in the Northern Territory (Tyler 1989).

Acknowledgments

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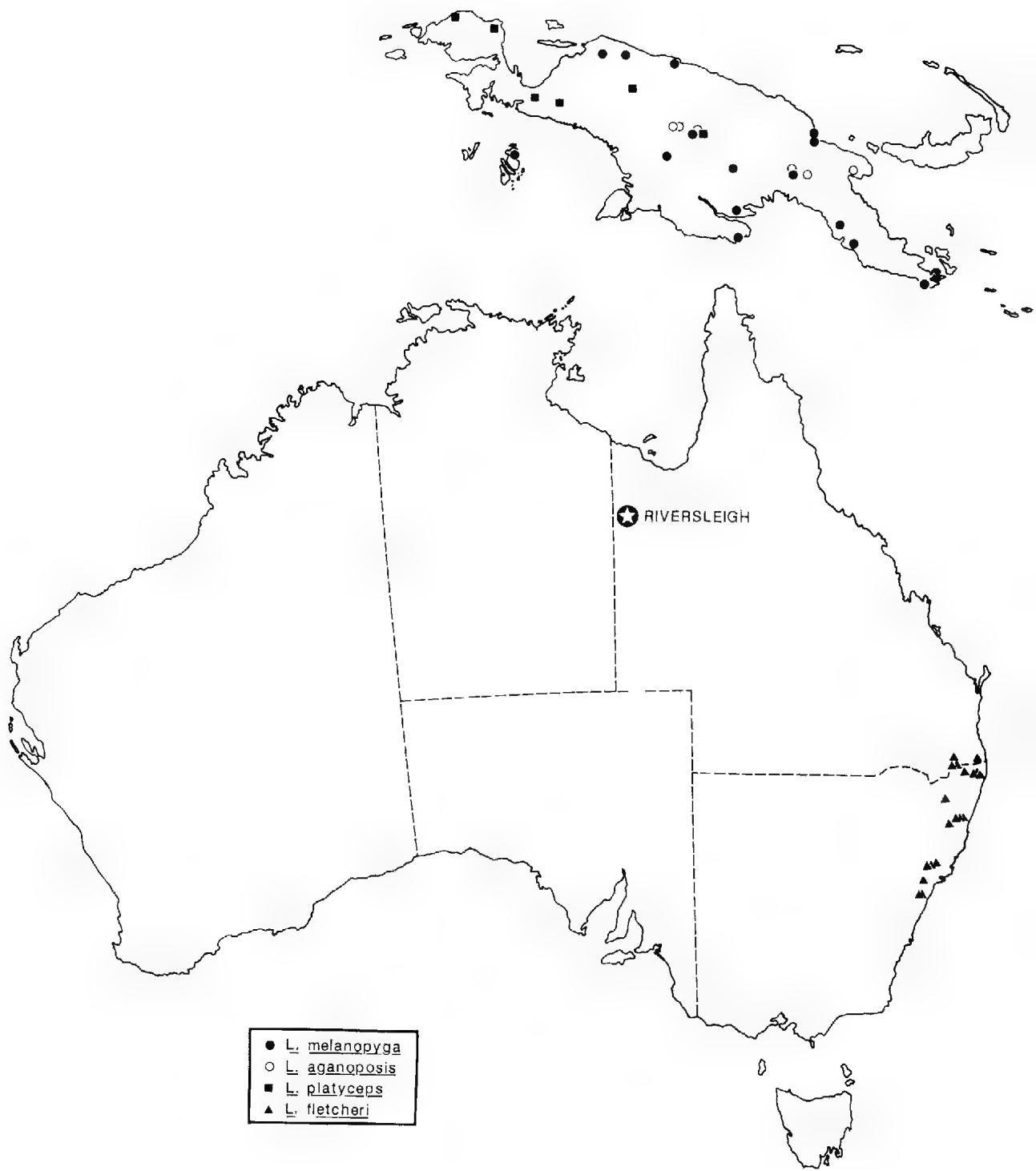


Fig. 6. Geographic distribution of *Lechriodus*.

TABLE 1. Size of *Lechriodus* species in millimetres. Snout to vent length data mostly obtained from Zweifel (1972). Snout to vent length of donor *L. aganopsis* unknown, and maximum length of *L. intergerivus* extrapolated from Fig. 4.

species	snout-vent length		size of donor	largest ilium examined	DAE-VAE	acet. fossa diam.
	♂ ♂	♀ ♀				
<i>aganopsis</i>	64-73	66-77	—	24.2	8.1	3.5
<i>fletcheri</i>	42-48	45-54	42	16.3	4.2	1.9
<i>intergerivus</i>	max. 41		?37.5	14.4	4.0	1.7
<i>melanopyga</i>	38-47	46-60	52	20.7	6.0	2.6
<i>platiceps</i>	64-78	72-95	67	24.0	7.8	3.8

played a vital role in that she undertook the cataloguing and initial sorting of material, and prepared Figures 1-2 and 4-6.

Dr R. G. Zweifel and Dr C. W. Myers (American Museum of Natural History) lent ilia of extant species and provided data about them, and Mr J. I. Menzies (National Museum & Art Gallery, Konedobu) provided distribution records from Papua New Guinea. Mr P. Kempster prepared Figure 3.

I am also indebted to Dr Keith Walker and Dr Margaret Davies for valuable discussions, and to the University of Adelaide for the provision of research facilities.

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OVER-SUMMERING REFUGES OF AQUATIC MACROINVERTEBMTES IN TWO INTERMITTENT STREAMS IN CENTRAL VICTORIA

*BY A. J. BOULTON**

Summary

Eight potential refuges for macroinvertebrates were sampled in two intermittent streams in central Victoria, Australia, during summer 1982-83 and summer 1983-84. Ninety-one aquatic taxa, mostly insects, were recorded. Receding pools harboured nearly three-quarters of these taxa; comparatively few were collected from the hyporheos or the water in crayfish burrows. Almost half the taxa were from refuges that did not hold free water. Macroinvertebrates persisted as desiccation-tolerant eggs (mayflies), larvae (chironomids and some beetles) or adults (beetles).

There was remarkable similarity between the broad taxonomic representation in these refuges and those described for intermittent streams in Ontario, Canada.

KEY WORDS: Intermittent streams, over-summering refuges, aquatic macroinvertebrates, Victoria, Australia, pholeteros, hyporheos.

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by A. J. BOULTON*

Summary

BOULTON, A. J. (1989) Over-summering refuges of aquatic macroinvertebrates in two intermittent streams in Victoria. *Trans. R. Soc. S. Aust.* 113, 23–34, 31 May, 1989.

Eight potential refuges for macroinvertebrates were sampled in two intermittent streams in central Victoria, Australia, during summer 1982–83 and summer 1983–84. Ninety-one aquatic taxa, mostly insects, were recorded. Receding pools harboured nearly three-quarters of these taxa; comparatively few were collected from the hyporheos or the water in crayfish burrows. Almost half the taxa were from refuges that did not hold free water. Macroinvertebrates persisted as desiccation-tolerant eggs (mayflies), larvae (chironomids and some beetles) or adults (beetles).

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Introduction

Ephemeral (episodic) and intermittent rivers and streams drain over half of the Australian mainland (W.D. Williams 1983) but despite their ubiquity and scientific interest, these systems have attracted little limnological attention (Boulton & Suter 1986; Boulton & Lake 1988). The situation is little better elsewhere (Williams 1987).

In intermittent streams, loss of water during the dry season is probably the most influential environmental parameter affecting the aquatic biota and has led to a wide range of physiological and behavioural adaptations (reviewed by Williams 1987). Behavioural avoidance appears to play a major part in the survival of many stream invertebrates during drought. Williams & Hynes (1977) recognized eight distinct types of refuges that were used by the fauna of a temporary stream in Ontario during summer and suggested that members of certain major taxonomic groups tended to over-summer at similar stages in their life cycle. For example, Ephemeroptera and most Chironomidae over-summered as eggs whereas Gastropoda, some Odonata, Hemiptera, and Coleoptera survived the dry period as adults (Williams & Hynes 1977).

In temperate Australian intermittent streams, recolonization pathways and potential over-summering refuges have never been investigated and little is known about the physiological or behavioural adaptations exhibited by the aquatic

biota (Boulton & Lake 1988). This study was aimed at elucidating over-summering strategies of aquatic macroinvertebrates in two intermittent streams in Victoria. I also was interested to see how closely the strategies used by biota in the intermittent Victorian streams matched those described by Williams & Hynes (1977) based on work done on intermittent streams in the northern hemisphere.

Materials and Methods

Study Area

Two study sites were located on the upper reaches of the Werribee River and two more on its main tributary, the Lerderderg River (Fig. 1). Both rivers arise on the southern edge of the Great Dividing Range approximately 100 km north-west of Melbourne and flow south-east before joining near Bacchus Marsh, north-west of Melbourne. Details of flow regime and catchment vegetation are given in Boulton & Smith (1985); other physicochemical data are presented in Boulton & Suter (1986).

The two rivers differ in permanency: the Werribee River ceases flow almost annually whereas the Lerderderg River flows throughout summer for one year in three. On average, the Werribee River does not flow for nine weeks while the Lerderderg ceases flow for six. The Werribee River did not flow at all at one site (Spargo Creek, SC) during the 1982 drought and only flowed for five months (late June to late November) at the site downstream (Werribee Picnic Spot, WPS). The study pool at WPS dried up completely during the ensuing summer. The following year, flow commenced in late June and continued for seven and a half months at both sites.

Flow started in late May 1982 at both sites (Fireplace Ford, FF and Wheeler Road, WR) on the

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Lerderderg River and ceased in early December. At FF, the study pool dried to a moist patch of leaves and water did not appear in the depression until mid-March 1983. At WR, the study pool was dry for six weeks before it also refilled in mid-March; flow resumed at both sites in early May, continuing over the following summer.

Physicochemical Monitoring of Potential Refuges

On 20.i.1983, diel ranges of temperature in and around a receding pool at WPS were measured using a 9-channel Miniature Intermittent Temperature Recorder (Grant Instruments, Cambridge, England). Thermistors were placed in shallow (5 cm) and deep (45 cm) water, below leaf litter, beneath a large flat rock, in the water of a crayfish (*Engaeus* sp.) burrow and in exposed grass in direct sunlight (regarded as "air temperature" cf. normal meteorological practise). Recording commenced at 5.00 a.m. and ceased at midnight.

At other times, spot water temperatures (mercury thermometer), dissolved oxygen (oxygen probe, Model 51A, Y.S.I., Yellow Springs, Ohio),

conductivity (conductivity meter, Radiometer, Denmark) and pH (Metrohm pH meter, Model CH9100, England) were measured when potential refuges containing free water were sampled. Conductivity data were converted to values at 18°C (K₁₈) (Bayly & Williams 1973) whereas dissolved oxygen was expressed as percentage saturation using the conversion table in Bayly & Williams (1973) and an appropriate correction factor for altitude.

Biological Sampling of Potential Refuges

A variety of collecting techniques was necessary to sample the diverse range of potential refuges:

(a) An F.B.A. pond-net (300 µm mesh) was used to sample fauna in the receding pools. I vigorously shuffled along the bottom of the pool, sweeping the net from side to side across the disturbed path for 30 seconds for each sample. The size of the pool limited the number of samples that could be collected; while I was keen to ascertain the relative abundance of the fauna, I did not want to deplete the remnant populations. A nearby permanent lake (Shaws Lake, Fig. 1) was sampled similarly.

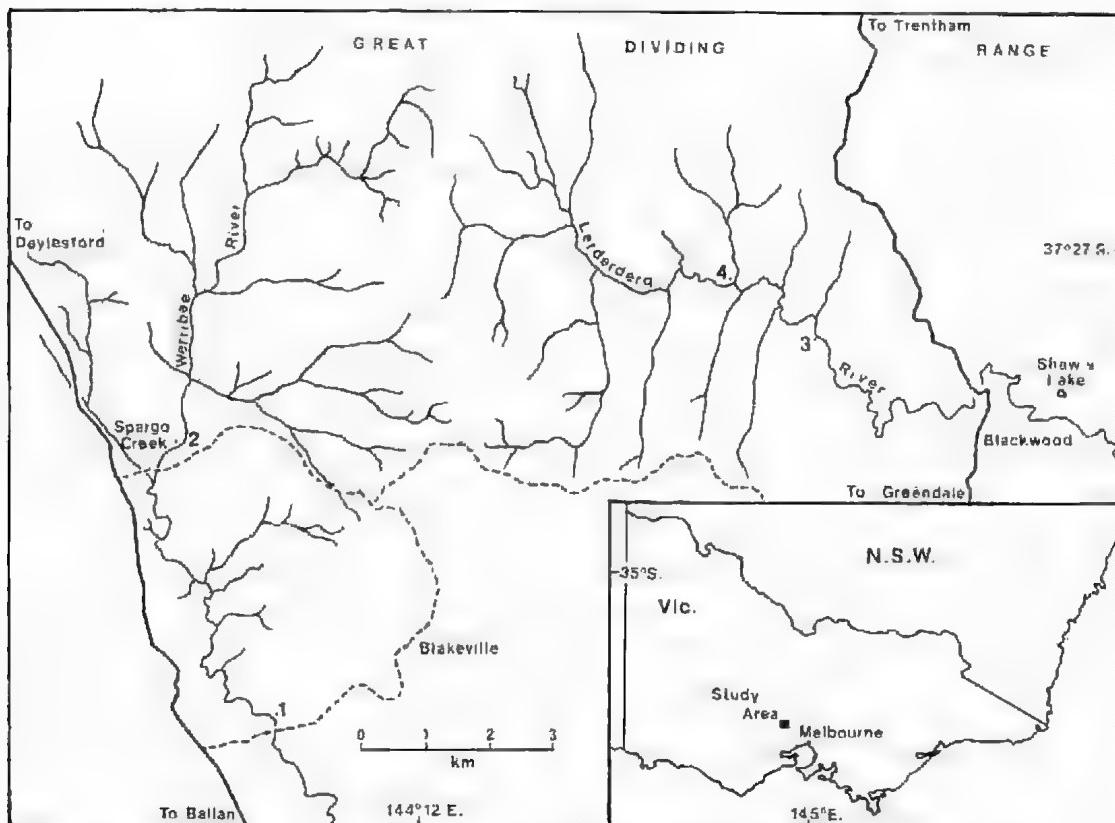


Fig. 1 Map of the study area showing the locations of the four study sites: Wernbee Picnic Spot (WPS) = 1, Spargo Creek (SC) = 2, Fireplace Ford (FF) = 3, Wheeler Road (WR) = 4.

(b) Animals residing in the water in crayfish (*Engaeus* sp.) burrows ("pholeteros" *sensu* Lake 1977) were collected by carefully excavating the burrow opening and lowering a flexible plastic tube (6 mm internal diameter) into the burrow water which was sucked out into a plastic bag. In the laboratory, this water was sieved (50 µm) with frequent washing to remove fine silt.

(c) The hyporheos was sampled by digging holes in the dry stream bed and sweeping a small hand-net (50 µm mesh) through the seepage. In some cases, it was necessary to use a plastic tube to collect the water. Quantitative sampling of this habitat was not attempted.

(d) Other potential refuges that were qualitatively sampled while the streams were dry included the humid microhabitats beneath rocks, stumps and mats of leaf litter and dried filamentous algae, and among the roots of riparian plants (e.g. *Carex* spp., *Leptospermum lanigerum*) and stranded *Myriophyllum propinquum* (water milfoil) and *Triglochin procera* (water ribbon). Rotting wood was broken open and examined, and strips of bark were peeled from exposed water-logged snags. Pieces of decomposed wood were brought back to the laboratory for microscopic inspection.

(e) Plastic bags were filled with surface (upper 10 cm) substrata and organic matter collected from the dry beds of riffles and pools. The water content of a subsample of the substratum was determined by subtracting the oven-dry weight (constant weight achieved after 48 h at 100°C) from the initial weight and expressing the value as a percentage. It was

was recorded. This process was repeated until no further species were seen. Subsequently, samples were taken at irregular intervals over the next fortnight, always returning the specimens to the tank. Some aquaria were maintained for several months to rear hatchlings through to adults to assist identification.

were identified as far as practicable (see Acknowledgments). Abundance was expressed qualitatively as "present" (1–2 individuals), "common" (3–10) or "abundant" (>10); given the variety of collecting methods and the uneven sampling effort, more precise quantification was inappropriate.

Results

Physicochemical conditions in potential refuges

Means and ranges of spot water temperature, pH, dissolved oxygen and conductivity in two refuges that held free water when they were sampled are listed in Table 1. Not surprisingly, the ranges of these variables were greater in the receding pools than in the burrow water of crayfish (Table 1). Hyporheic water was too disturbed during sampling to obtain reliable physicochemical data and data from Shaws Lake are too few to be useful.

Continuous records of water temperature in a receding pool at WPS illustrated the diel fluctuation of temperatures in various refuges (Fig. 2). Air temperature in direct sunlight near the pool ranged from 3.5°C at dawn to 35°C early in the afternoon (Fig. 2). The day was fine and clear with a light south-easterly breeze starting at 2.30 p.m. Sunrise

TABLE 1. Means and ranges of water temperature, pH, dissolved oxygen and conductivity in two potential oversummering refuges, based upon n spot measurements

Refuge		Water Temperature (°C)	pH	Dissolved Oxygen (% saturation)	Conductivity (K ₁₀) (µS/cm)
Receding pools	̄	13	6.4	30.4	164
	range	7–25	4.7–7.2	6–78	90–290
	n	25	23	25	25
Crayfish burrow water	̄	9.3	5.8	63	88
	range	7–12	5.2–6.2	45–79	66–110
	n	8	8	8	8

assumed that all weight lost during incubation was due to the evaporation of water.

The rest of the sample was emptied into an aquarium immediately upon return to the laboratory and flooded with dechlorinated tap water. Within 30 minutes of immersion of the substrata, a hand-net (50 µm mesh) was swept vigorously through the tank and the live contents examined using an Olympus stereomicroscope, and the rank abundance of all invertebrates present

was at 6.21 a.m. but the pool was shaded by surrounding forest until about 9.00 a.m. Sunset was at 8.41 p.m.

Water temperature in the shallows (5 cm) lagged closely behind air temperature (Fig. 2a) while in deeper water (45 cm) the daily range was far less (Fig. 2b). Water in a crayfish burrow exhibited a diel range of less than 3°C (Fig. 2b). The insulative capacity of several centimetres of eucalypt litter and dried filamentous algal mat approximated that of

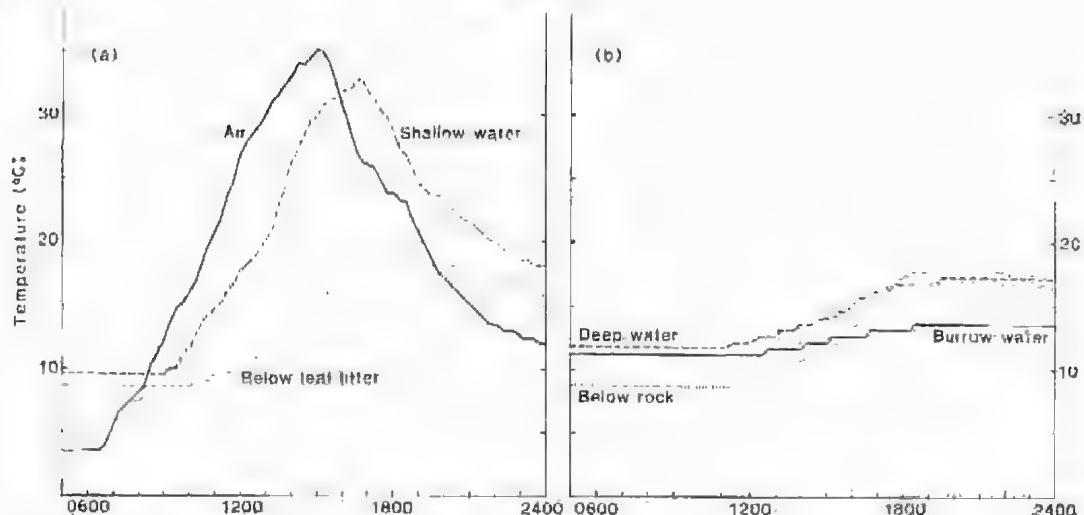


Fig. 2 Variation in water temperature of several potential over-summering refuges in and around the study pool at WPS on 20.i.1983. See text for details.

a flat rock 15 cm thick (cf. Figs 2a and b). During the day, conductivity remained at 270 $\mu\text{S}/\text{cm}$ and pH ranged from 5.5 to 6.1 ($n = 6$ determinations, mean pH = 5.6).

Aquatic macroinvertebrates collected from potential refuges

A total of 91 taxa was collected from the eight over-summering refuges sampled at four sites on the Werribee and Lerderderg Rivers (Table 2). Nearly three-quarters of these taxa over-summered in receding pools along the river beds. These pools also harboured tadpoles of *Litoria ewingi* (Duméril & Bibron) (Hylidae) and *Neobatrachus sudelli* (Lamb) (Leptodactylidae); large numbers of the latter perished when the pool at WPS dried up over the summer 1982–83. Several specimens of *Galaxias olidus* Günther (Pisces: Galaxiidae) were collected from the same pool.

Few taxa were recorded from the hyporheos or crayfish burrow water (Table 2); individuals in these habitats were usually tiny. Decomposed wood yielded small oligochaetes, tipulids and boring chironomids (Orthocladiinae) while amphipods (*Austrochiltonia australis*) were found in curled up strips of *Eucalyptus* spp. bark near the margins of dried out pools. These habitats were not sampled intensively and it is likely that other taxa (e.g. helminthid beetles) may also use rotting wood as a refuge over summer.

Almost half of the taxa recorded were collected from refuges that did not hold free water when sampled (Table 2). Some of these (e.g. *Nousia* spp. and ?*Dinotoperla thwaitesi*) apparently hatched from desiccation-resistant eggs whereas others

survived as larvae (chironomids, psephenids, helminthids and case-building caddisflies) or as adults (dytiscids and helminthids) in moist microhabitats below rocks or mats of leaf litter and dried filamentous algae. Large numbers of microcrustacea (ostracods, harpacticoid and cyclopoid copepods) were recovered from dry substrata flooded in the laboratory. The water content of these samples was usually less than 10% by weight (range = 0.19–74.00%, mean = 7.71%, S.E. = 0.93%, $n = 53$) and did not differ significantly between samples collected from the beds of the pool and riffle habitats (Mann-Whitney U-test, $p > 0.05$).

Comparisons among the refuges should be made cautiously because the collecting techniques and the numbers of samples taken from each habitat differed substantially. For this reason, I did not attempt calculations of coefficients of similarity of faunal composition among refuges.

Discussion

The classification of over-summering refuges used by aquatic macroinvertebrates in temporary streams in Ontario (Fig. 3 in Williams & Hynes 1977) may be applied usefully to the data from the Werribee and Lerderderg Rivers. At a broad taxonomic level, the faunal elements over-summering in the various refuges are almost identical and do so at similar stages of their life cycle. This may seem unexpected given the differences in latitude, source of stream flow (snowmelt in Ontario, rainfall in this study) and the difference in the degree of species overlap with nearby permanent streams (Boulton & Sitter 1986;

TABLE 2. Aquatic taxa recorded from potential refuges sampled over the 1982-1983 summer when the streams had ceased flow. Dead specimens were omitted. Abundance categories are qualitative (+ = present (1-2 individuals), C = common (3-10 individuals), A = abundant (more than 10 individuals) because of the different sampling frequency (n) and methodology (see text). * These individuals did not grow to identifiable size in the laboratory. ** (NMV sp.n) refers to the number of the specimen held in the voucher collection of the Museums of Victoria.

Refuge	Below dried litter (n)	Crayfish (Engaeus sp.) (7)	Receding burrows (12)	Shaws pools (23)	Lake (2)	Wood and bark (10)	Dry substrata flooded in laboratory riffle pool (47) (14)	Hyporheos (5)
TURBELLARIA								
Neorhabdocoela								
?Mesostoma sp.					+			
Tricladida								
<i>Cura pinguis</i> (Weiss)					C	C		
NEMATODA								
Nematoda spp.	+		C		A	C	A	A
GASTROPODA								
Hydrobiidae								
<i>Angrobia</i> sp.					A		C	+
<i>Glacidorbis hedleyi</i> Iredale							+	
Ancylidae								
<i>Ferrissia</i> spp.	+				C			+
Planorbidae								
<i>Physastra gibbosa</i> (Gould)					A	A		
BIVALVIA								
Sphaeriidae						C		
<i>Sphaerium tasmanicum</i> (Tenison-Woods)								
OLIGOCHAETA								
Oligochaeta spp.	C	C		A	A	C	A	A
CRUSTACEA								
Janiridae								
<i>Heterias</i> sp.			C					+
Ceinidae								
<i>Austrochiltonia australis</i> (Sayce)	A			A	C	C		
Atyidae								
<i>Paratya australiensis</i> Kemp						C		
Parastacidae								
<i>Cherax destructor</i> Clark	+		C		C	C		
<i>Engaeus</i> sp.								
HYDRACARINA								
Limnesiidae								
<i>Limnesia</i> spp.				+		C		
Hygrobatidae								
<i>Australiobates</i> spp.			C					
<i>Corticacarus</i> spp.			C		+		A	+
Mesostigmata								+
Aquatic sp.								+
EPHEMEROPTERA								
Leptophlebiidae								
<i>Nousia</i> spp.			C		C		A	A
<i>Atalophlebia</i> sp.			C		A			+
ODONATA								
Lestidae								
<i>Austrolestes</i> ?io (Selys)				+				
Corduliidae								
<i>Hemicordulia</i> ?tau Selys				+				

Refuge	Below dried litter	Crayfish burrows (<i>Engaeus</i> sp.)	Receding pools	Shaws Lake	Wood and bark	Dry substrata flooded in laboratory	Hyporheos riffle pool	
(n)	(7)	(12)	(23)	(2)	(10)	(47)	(14)	(5)
PLECOPTERA								
Austroperlidae						+		
<i>Acroperla atra</i> (Samal)								
Notonemouridae								
<i>Astrocerca tasmanica</i> (Tillyard)					A			
Gripopterygidac								
<i>?Dinotoperla thwaitesi</i> *Kimmmins								+
							C	C
HEMIPTERA								
Veliidae								
<i>Microvelia dubia</i> Hale					+	C		
<i>M. distincta</i> Malipatil					C			
Notonectidae								
<i>Anisops deanei</i> Brooks					+	C		
<i>A. ?hackeri</i> Brooks					+			
Corixidae								
<i>Microdictyon annae illiesi</i>					C			
Wróblewski								
<i>M. a. tasmanica</i> Wróblewski					+			
COLEOPTERA								
Dytiscidae								
<i>Antiporus blakei</i> (Clark)					C	C		
<i>A. femoralis</i> (Boheman)					A			
<i>Chostonectes johnsoni</i> (Clark)					+			
<i>Chostonectes</i> spp. larvae					C			
<i>Copelatus australiae</i> Clark	C							
<i>Hyderodes schuckardi</i> Hope	+							
<i>Lancetes lanceolatus</i> (Clark)	+				+			
<i>Liodessus shuckardi</i> (Clark)					+			
<i>Necterosoma penicillatum</i> (Clark)					A	C		+
<i>Necterosoma</i> sp. larvae					+			
<i>Platynectes decempunctatus</i>	C				+			
(Fabricius)								
<i>Rhantus suturalis</i> (Macleay)					+	I		
<i>Sternopriscus mundanus</i> Watts					C			
Gyrinidae								
<i>Macrogyrus</i> sp.					+			
Hydraenidae								
<i>Hydraena luridipennis</i> Macleay					+			
<i>H. ?tricantha</i> Zwick					+			
Helodidae								
Helodidae sp. larvae							I	
Psephenidae								
<i>Scleroclyphon striatus</i>								
Lea larvae	+							+
Helminthidae								
<i>Austrolimnius hebrus</i> Hinton					+			
<i>A. maro</i> Hinton					+	A	C	
<i>A. "mormo"</i> larvae (NMV sp.								
H ₂)**								
<i>Austrolimnius</i> sp. larvae						A	C	
<i>Simsonia tasmanica</i> (Blackburn)						C	C	
laryae								-
DIPTERA								
Tipulidae								
<i>Limonia</i> sp.							+	
<i>Ormosia</i> sp.							+	
Psychodidae								
<i>Psychoda</i> sp. (NMV sp. 3)**						I	C	

Refuge	Below dried litter (n)	Crayfish burrows (7)	Receding pools (12)	Shaws Lake (23)	Wood and bark (2)	Dry substrata flooded in laboratory (10)	Riffle pool (47)	Hyporheos pool (14)	
Culicidae									
<i>Aedes</i> spp.					A	C			
<i>Anopheles annulipes</i> Walker					C				
<i>Culex fatigans</i> Weidmann					C				
<i>C. annulirostris</i> Skuse					+				
<i>C. australicus</i> Skuse					+				
Chironomidae									
<i>Ablabesmyia</i> sp. 1 (NMV sp. 7E)**					C	+			
<i>Ablabesmyia</i> sp. 2 (NMV sp. 66E)**					+				
<i>Paramerina</i> spp. (nr NMV sp. 32E)**					C				
<i>Chironomus</i> nr <i>februario</i> (NMV sp. 136E)**					C	+			
<i>Einfeldia</i> sp.					+				
nr <i>Dicrotendipes</i> sp. (NMV sp. 34E)**					C				
<i>Riethia</i> sp. (NMV sp. 5E)**					+			+	
<i>Stenochironomus</i> sp. (NMV sp. 3E)**									
<i>Calopsectra</i> sp. (NMV sp. 22E)**					C	C		+	
<i>Stempellina</i> nr <i>bausei</i>					+			+	
nr <i>Monodiamesa</i> sp.							C	+	
<i>Orthocladius-Cricotopus</i> complex (includes NMV spp. 12E and 160E).									
<i>Heterotriassocladius</i> sp.		+			C				
Tiny chironomids*			+		C	A			
Ceratopogonidae									
<i>Bezzia</i> sp.								+	
<i>Nilobezzia</i> sp.								+	
Stratiomyidae									
Stratiomyidae spp.		+			C	+		C	
Empididae									
Empididae spp.			+		C			+	
Dolichopodidae									
Dolichopodidae sp.								+	
Muscidae									
Muscidae spp.					C	+		+	
TRICHOPTERA									
Hydrobiosidae									
<i>Ptychobiosis nigrita</i> (Banks)					+				
Hydropsychidae									
<i>Hellyethira ?simplex</i> (Mosely)					+				
Calocidae									
Calocidae sp.								+	
Leptoceridae									
<i>Leptorussa darlingtoni</i> (Banks)					C			+	
<i>Oecetis</i> sp.					C				
<i>Lectrides varians</i> Mosely		C			C				
<i>Tripectides similis</i> Mosely					C				
<i>T. truncatus</i> Mosely		+			C				
Tiny leptocerids*					C				
Total number of taxa	91	15	6	68	23	4	27	24.0	.8
% of total number of taxa		16.5	6.6	74.7	25.3	4.4	29.7	26.4	.8.8

Boulton & Lake 1988). However, physiological and behavioural adaptations employed by animals of common heritage that share gross morphological similarities and that are subjected to similar environmental selective pressures are likely to converge upon a restricted number of solutions (parallel evolution *sensu* Mayr 1963).

In the Werribee and Lerderderg Rivers, several common taxa (*Nousia* sp., some gripopterygid stoneflies) apparently hatched from desiccation-resistant eggs (cf. Lehmkühl 1971; Snellen & Stewart 1979; Malicky 1982) and were among the first invertebrates to appear when flow resumed. Similar findings have been reported in other intermittent streams (Harrison 1966; Chutter 1968; Hynes 1975; Ladle & Bass 1975; Williams & Hynes 1976, 1977; Abell 1984; Towns 1985). Although simuliids (Diptera) were also common shortly after flow resumed in the Werribee and Lerderderg Rivers, none emerged from the dry substrata flooded in the laboratory, implying that eggs are laid by adults flying in when flow starts (cf. Hynes 1975; Abell 1984).

Mitucrustacea (ostracods, cyclopoid and harpacticoid copepods) emerged within hours of flooding dry substrata in the laboratory and harpacticoid copepods were observed mating a day later. Morton & Bayly (1977) recovered ovigerous harpacticoid females only 24 hours after flooding some dried mud from a temporary pool at Clayton, Victoria, suggesting that some species diapause at an advanced stage of development (cf. Cole 1953). Another taxon, common shortly after dry substrata were inundated, was a neorhabdoecel tentatively identified as *Mesostoma* sp.. Bayly (1970) recorded *Mesostoma* from a temporary saline lake in south-eastern Australia and observed thick-shelled eggs in the uteri of some specimens that are apparently released when the animals die. A similar strategy for desiccation-tolerance has been observed in neorhabdoecels from a temporary ditch in England (Cox & Young 1974).

Gastropods in the Werribee and Lerderderg Rivers survive drought either by secreting a protective epiphram (e.g. *Physastra gibbosa*, *Ferrissia* spp.) (cf. Kenk 1949; Eckblad 1973; Legier & Talin 1973) or by closing their operculum (e.g. *Angrobia* sp. and *Glacidorbis hedleyi*) (Boulton & Smith 1985). Most tended to aestivate in moist microhabitats under stumps, dry algal mats and leaf litter (cf. Strandine 1941; Klekowski 1959; Casey & Ladle 1976). The bivalve *Sphaerium tasmanicum* probably minimizes water loss by closing its valves. Other members of the Sphaeriidae are ovoviparous and brood their young while surface water is absent (Heard 1977; Hornbach *et al.* 1980; McKee & Mackie 1981). Aestivating juveniles have

been found buried in the substratum (Way *et al.* 1980) but I did not recover any from my study sites.

Parastacid crayfish found in the Werribee River over-summer in their burrows where water temperatures remain quite constant. Surprisingly few other invertebrates (pholeteros *sensu* Lake 1977) appear to use this refuge (cf. Creaser 1931; Williams *et al.* 1974; Williams & Hynes 1976; Wiggins *et al.* 1980). The pholeteros in other Victorian *Engaeus* spp. burrows is also depauperate (Horwitz *et al.* 1985). Nevertheless, this refuge seems to be important for the survival of janirid isopods in the Werribee River. Isopods usually are absent from temporary waters because they lack desiccation-resistant stages and are sedentary (Williams 1985). The water in burrows constructed by fish serves as sources of recolonists after droughts in some streams overseas (e.g. Tramer 1977; Glodek 1978) but this refuge was not evident in the Werribee and Lerderderg Rivers.

Few taxa were abundant in the hyporheos of the study sites during summer. This paucity may reflect the crude sampling methods because amphipods, janirid isopods, stoneflies, molluscs and oligochaetes have been recorded from the hyporheos of the intermittent Brachina River in South Australia (W.D. Williams 1983). Overseas, the hyporheos is considered to be an important refuge from both droughts and floods in some temporary and permanent streams (Clifford 1966; Williams & Hynes 1977; Williams 1977, 1984). However, in desert streams whose beds are mainly composed of unstable sand, hyporheic dormant stages are rare because of high temperatures in the dry streambed and severe scouring of the channel during flash floods (Gray 1981, Fisher *et al.* 1982).

One refuge not considered by Williams & Hynes (1977), possibly uncommon in Ontario, is that provided by decomposing wood debris, abundant along the banks and stream beds of many Australian intermittent streams. In my study, this refuge harboured oligochaetes, amphipods, tipulids and chironomids. More intensive sampling is likely to yield further taxa because other workers have recorded large numbers of xylophilous taxa from permanent streams in Oregon (Anderson *et al.* 1978; Dudley & Anderson 1978) and New Zealand (Anderson 1982).

In the Werribee and Lerderderg Rivers, taxa aestivated under rocks and mats of algae (where temperatures remained constant) as adults (e.g. amphipods, dytiscids) or larvae (e.g. chironomids, stratiomyids). Some larval stages seemed surprisingly tolerant of desiccation; for example, a large water penny larva (*Sclerocyphus striatus*), collected from the exposed surface of a flat rock on the bed of a riffle that had not flowed for 13

weeks, resumed activity immediately after immersion in water from a nearby pool. Similar tolerance of desiccation by larvae of *Sclerocyphus* spp. has been described in Tasmania (Smith 1981) and Queensland (Smith & Pearson 1985).

Adult aquatic Hemiptera (e.g. corixids, notonectids) and Coleoptera (e.g. dytiscids) probably fly in from nearby permanent waters. Such aerial recolonization of temporary pools and streams by these groups is commonplace (e.g. Fernando 1958, 1959; Fernando & Galbraith 1973; Williams & Hynes 1976, 1977; Wiggins *et al.* 1980; Abell 1984; Williams 1985). I also found several species of adult dytiscids over-summering below rocks and dry litter near the margins of pools at SC and WPS. This strategy seems less well-known for this group; only D.D. Williams (1983), Boumezzough (1983) and McKaige (1980)¹ (in a temporary pond near Colac, western Victoria) have reported similar observations.

Although the receding pools harboured most of the taxa that over-summer at the study sites, they appeared to be the most physicochemically "harsh" refuge that I sampled. The pools experienced a considerable diel range in water temperature, oxygen levels were frequently below 20% saturation and pH levels fell to less than 5. Conductivity rises as the water evaporates and the pools are often stained dark brown with eucalypt leachate. Similar conditions have been observed in receding pools in other intermittent streams in Australia (Towns 1983, 1985; Smith & Pearson 1987) and North America (Slack 1955; Larimore *et al.* 1959; Clifford 1966; Harrel & Dorris 1968).

The invertebrates that over-summer in these pools have various adaptations that allow them to tolerate such physicochemical extremes. For example, larval dytiscids come up to the surface of the pool to obtain air through the terminal abdominal spiracle whereas adult dytiscids store air beneath their elytra (Britton 1970). Some chironomid larvae (e.g. *Chironomus lit. febrarius*) are particularly abundant in the receding pools and use haemoglobin to facilitate oxygen uptake (Colless & McAlpine 1970). Mayfly nymphs (*Atalophlebia* sp.), also common in this refuge, have large gills that are constantly oscillated to enhance respiration (Boulton & Lake 1988). Terrestrial oviposition by two species of leptocerid caddisfly common in the Lerderderg River (*Leptorissa darlingtoni* and *Lecrides varians*) may also be an adaptation to low or unpredictably fluctuating oxygen levels (Towns 1983). Development of vulnerable juvenile stages

in a physicochemically harsh environment may be avoided or accelerated by ovoviparity exemplified by the stoney *Austrocerco tasmaniensis*, also recorded by Towns (1985) in a South Australian intermittent stream.

Although there is little known about the thermal tolerances of aquatic macroinvertebrates in Australian intermittent streams, it appears that many taxa can cope with short-term exposure to extremes of water temperature. It is likely that they remain near the bottom of the pool where the temperatures may be as much as 15°C cooler than those of the surface water exemplified by the study pool at WPS. Such stratification is uncommon in shallow pools (e.g. Byars 1960; Butler 1963; Moore 1970; Hartland-Rowe 1972). However, Eriksen (1966) recorded surface-bottom differences of 9–16°C in temporary turbid puddles less than 50cm deep, and a shallow (10 cm) rockpool in a stream in the Pyrenees had a surface temperature of 29.9°C while the bottom was 19°C (Chodorowska & Chodorowski 1966). Less marked stratification in pools in North American intermittent streams has been reported by Neel (1951) and Slack (1955).

Isolated pools remaining in the stream bed are important over-summering refuges for aquatic macroinvertebrates in intermittent streams elsewhere (e.g. Slack 1955; Paloumpis 1958; Larimore *et al.* 1959; Williams & Hynes 1976; Abell 1984). In temporary streams in Ontario, they also provide excellent breeding environments due to the ease with which they warm up and the abundant plant food that develops within them, and they enable species with long-lived aquatic stages to complete their life-cycles (Williams & Hynes 1976). Similarly, in the Werribee and Lerderderg Rivers, these pools support a rich fauna although environmental conditions are harsh and predators are numerous (Boulton & Suter 1986).

Taxa whose aquatic life-spans are brief enough to be completed while water is present are under less selective pressure to adopt these strategies than species whose aquatic development takes longer than the period that water persists. Unfortunately, we lack information on the duration of aquatic stages of many Australian macroinvertebrates and few generalizations may be drawn. Most crustaceans and molluscs listed in Table 2 probably live longer than a year and this may account for their ability to survive in refuges other than the pools. Although many other taxa (e.g. chironomids, culicids) can complete their aquatic stages in a matter of weeks, their survival in intermittent streams depends upon when their eggs hatch and how long water persists afterwards. Interpretation of the significance of many of these refuges will be possible when more information on the life histories of

¹ McKaige, M.E. (1980) Emergence and development of aquatic invertebrate communities from dried mud after flooding. B.Sc. Hon thesis, Department of Zoology, Monash University. (Unpubl.).

macroinvertebrates in Australian intermittent streams is available.

In summary, there appear to be five major over-summering strategies employed by the fauna of these two rivers:

i) tolerating extreme and variable environmental conditions in the remaining pools,

ii) surviving in moist microhabitats below stones, stumps and mats of dried algae and leaf litter, and in rotting wood,

iii) over-summering in microhabitats where environmental conditions are relatively mild and constant such as in the hyporheos or the burrow water of crayfish,

iv) surviving as desiccation-resistant stages in the dry substratum, and,

v) living in nearby permanent water-bodies and flying in and ovipositing when flow resumes.

The relative contributions from each of these refuges reflects the nature of the substratum (e.g. Clifford 1966; Gray 1981), the amount and pattern of discharge during the previous spring, and the severity of the summer. This last was illustrated by the 1982 drought when all the pools in the upper reaches of the Werribee River dried completely, extinguishing several common taxa (e.g. the shrimp *Paratya australiensis*) that I never recorded the following year. Differential survival of fauna in these various refuges undoubtedly influences the community composition of the stream and has a profound effect upon its ecological succession during the ensuing period of flow.

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**THE LARVA AND NYMPH INSTARS OF *ODONTACARUS (LEOGONIUS)*
ADELAIDEAE (WOMERSLEY) (ACARINA: TROMBICULIDAE:
LEEUWENHOEKIINAE)**

BY R. V. SOUTHCOTT

Summary

The larva of *Odontacarus (Leogonius) adelaideae* (Womersley, 1944) is redescribed, and a lectotype designated. Larvae have been collected repeatedly on domestic cats in suburban Adelaide, South Australia, and reared experimentally to protonymphs and deutonymphs. The larva, protonymph and deutonymph are described. Experimental transfer of larvae from cats to man is described. A key is given to the known deutonymphs of *Leogonius*, and revisional notes on the classification of the larvae.

KEY WORDS: Taxonomy, *Odontacarus*, *Leogonius*, South Australia, larva, protonymph, deutonymph, rearing, cat.

THE LARVA AND NYMPH INSTARS OF *ODONTACARUS (LEOGONIUS)* *ADELAIDEAE* (WOMERSLEY) (ACARINA: TROMBICULIDAE: LEEUWENHOEKIIAE)

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Summary

SOUTHcott, R. V. (1989) The larva and nymph instars of *Odontacarus (Leogonius) adelaideae* (Womersley) (Acarina: Trombiculidae: Leeuwenhoekiiiae). *Trans. R. Soc. S. Aust.* 113(00), 35–45, 31 May, 1989.

The larva of *Odontacarus (Leogonius) adelaideae* (Womersley, 1944) is redescribed, and a lectotype designated. Larvae have been collected repeatedly on domestic cats in suburban Adelaide, South Australia, and reared experimentally to protonymphs and deutonymphs. The larva, protonymph and deutonymph are described. Experimental transfer of larvae from cats to man is described. A key is given to the known deutonymphs of *Leogonius*, and revisional notes on the classification of the larvae.

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Introduction

Womersley (1944) described *Leeuwenhoekia adelaideae* from several larval trombidioïd mites, collected from domestic cats in southern suburbs of Adelaide in 1931 and 1941, and three collected from rats, in Cairns, Queensland, in 1939. He had earlier (Womersley 1934) referred to some of the same (1931) larvae as "*Leuwenhoekia* (sic) *australiense* (sic) Hirst 1929" (sic), i.e. as *Leeuwenhoekia australiensis* Hirst, 1925, originally described from larvae collected at Ashfield, Sydney, New South Wales, but subsequently recorded more widely in Australia and the south-west Pacific area (Gunther 1952; Wharton & Fuller 1952).

Following revisions of the taxonomy of the leeuwenhoekiine larval mites, those known from Australia, New Guinea and south-east Asia (previously referred to *Leeuwenhoekia* Oudemans, 1911 and *Acomatacarus* Ewing, 1942) are referred to *Odontacarus* Ewing, 1929, subgenus *Leogonius* Vercammen-Grandjean, 1968 (see Southcott 1986a).

In the present paper the larva of *Odontacarus adelaideae* is redescribed. The first attempt to rear larvae was in 1941, but the protonymphs and deutonymphs described below were not obtained until 1950–1952.

A key is given for deutonymphs of *Leogonius*. The successful transfers of partly-fed larvae from cats to feeding on man is described.

Materials and Methods

Slide-mounted mites in the South Australian Museum Adelaide (SAM) referred to *O. adelaideae* and collected by D. C. Swan in 1931 and R. V. Southcott in 1941 were examined. They were originally mounted in gum-chloral media, but

showed evidence of extensive remounting to gum-chloral or polyvinyl alcohol-based media, with associated damage. Some specimens labelled as *adelaideae* from N.S.W. were excluded. The specimens recorded by Womersley (1944) from Cairns, Qld, 1939 were not located.

Further larvae were collected topotypically in 1941 and between 1946–1952 from the ears of domestic cats. Some were mounted in water-soluble media (generally gum-chloral based), whilst attempts were made to rear others to later instars.

In 1941 larvae freshly collected from cats were confined under a watch-glass attached to my forearm with adhesive strapping. Although the mites reattached and increased in size, no successful transformation occurred.

Mites were again collected from the ears of domestic cats from the same site, during summer-autumn of 1946–1952, and placed on strips of damp blotting paper in sealed tubes at ambient temperatures. In one case a nearly-intact protonymph was obtained. In several cases transformation to deutonymph occurred. All specimens were then preserved in lactic acid, or dry, until studied, generally 35–40 years later. The deutonymphs and residual pieces of larval or protonymphal pelts were slide-mounted, through lactic acid to Hoyer's gum chloral medium (Baker & Wharton 1952).

Microscopy was by a Leitz Ortholux microscope with phase-contrast and polarizing facilities; its camera lucida was used to make the line drawings.

Terminology and abbreviations are as in Southcott (1986a,b). All measurements are in μm unless otherwise stated. Prefixes: ACB to author's registration numbers, N to those of SAM.

Odontacarus Ewing

Odontacarus Ewing, 1929, p. 188

(for synonymy see Southcott, 1986a, p. 171, and contained references).

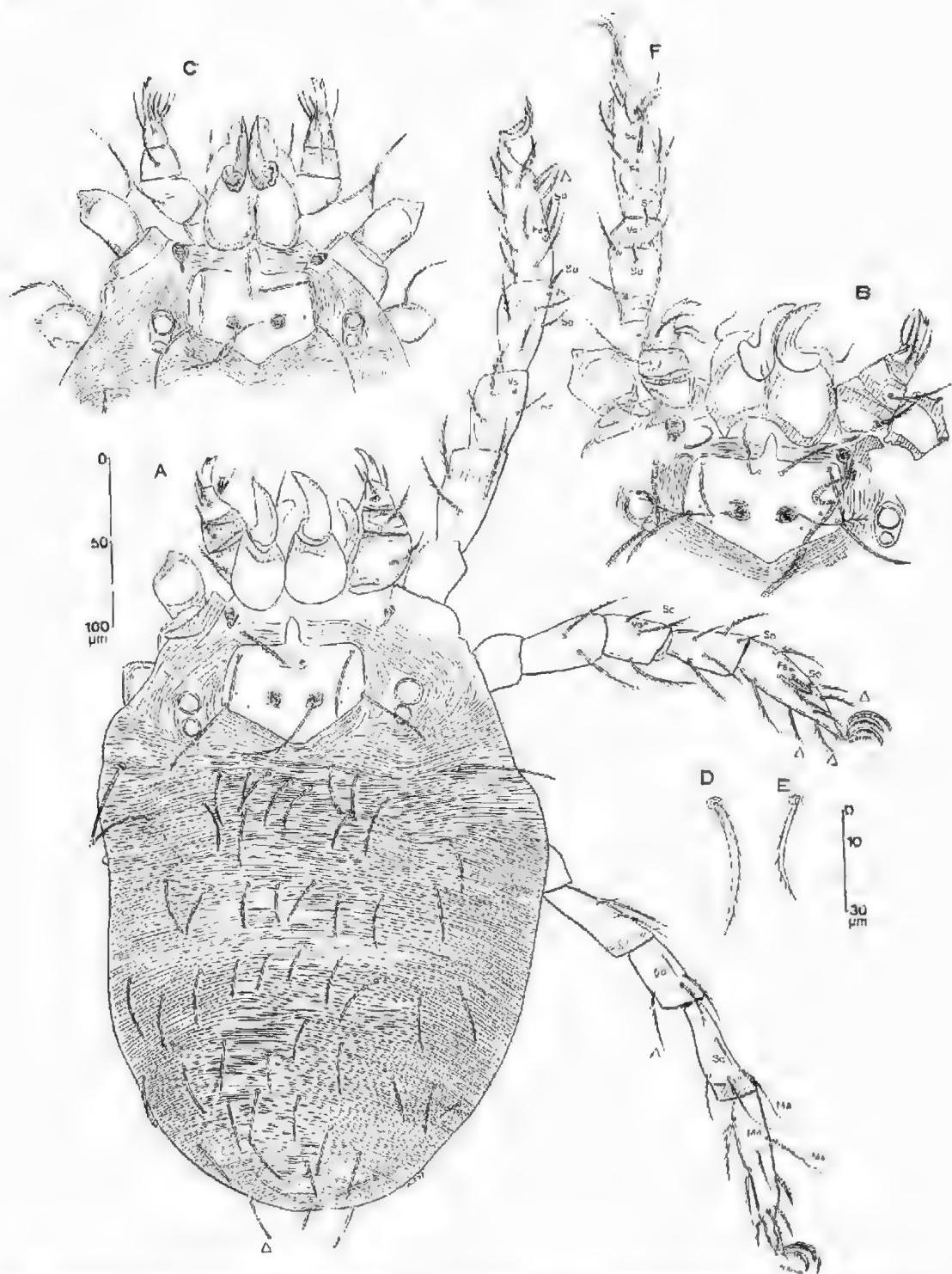


Fig. 1 *Odontacarus adelaideae* (Womersley), larva. A Dorsal view of lectotype, legs on left omitted beyond trochanter; legs on right completed from specimens in same postures as lectotype, leg I from specimen ACB520BA2, leg II from ACB270A, leg III from ACB270B. B Gnathosoma, dorsal scutum and adjacent structures from paralectotype N1988333 (ACB941). C Same for specimen ACB520BA2. D Dorsal idiosomal seta. E Ventral idiosomal seta. F Tibia I and tarus I, dorsal aspect, of paralectotype N1988333. (D, E to scale on right; other figures to scale on left).

Definition of larva: Trombidioidea (as defined by Southcott 1987) with anterior median dorsal setum, with nasus, two anteromedian setae, two anterolateral setae, two posterolateral setae, and two sensilla, each with non-expanded sensillary seta. Leg segmental formula 6, 6, 6. Eyes 2 + 2, sessile.

Definition of deutonymph and adult: Trombidioidea with anterior median crista, expanded anteriorly to a blunt arrow-head-like shape (sagitta), bearing two normal setae, with two sensilla towards its posterior end, each bearing a slender, setulose sensillary seta. Leg segmental formula 7, 7, 7. Deutonymph with two pairs of suckers (acetabula) along each lateral genital valve, adult with three pairs. Dorsal idiosomal setae not leaf-like, nor divided, but may be present in two distinct forms. Eyes absent.

Type species: *Trombicula dentata* Ewing, 1925, p. 257.

Subgenus *Leogonius* Vercammen-Grandjean, 1968

Definition of larva: as in Gill (1979, p. 143).

Type species: *Leeuwenhoekia australiensis* Hirst, 1925, p. 150.

Odontocarus adelaideae (Womersley)

FIGS 1A-E, 2-6

Leeuwenhoekia (sic) *australiense*: (sic) Womersley, 1934, p. 217 (partim).

Leeuwenhoekia australiensis: (sic) Womersley, 1937, p. 82 (partim).

Leeuwenhoekia australiensis: Womersley & Headliff, 1943, p. 141 (partim); Thor & Willmann, 1947, p. 323 (partim).

Leeuwenhoekia adelaideae Womersley, 1944, p. 105; Gill, Moule & Riek, 1945, p. 29; Gill & Parrish, 1945, Plate 3; Taylor, 1946, p. 228.

Acomatacarus adelaideae: Womersley, 1945, pp. 98, III; Southcott, 1957, p. 149.

Acomatacarus (*Acomatacarus*). *adelaideae*: Wharton & Fuller, 1952, p. 97.

Odontocarus adelaideae: Southcott, 1973, pp. 46, 103; 1976, p. 139; 1978, p. 16 (unnamed); Lee & Southcott, 1979, p. 35; 1980, p. 7.

Odontocarus (Leogonius) adelaideae: Southcott, 1986a, p. 180.

Description of larva: *Lectotype*: Colour in life orange red. Length of idiosoma (mounted on slide) 370, width 285; total length from tip of cheliceral fangs to posterior pole of idiosoma 463.

Dorsal scutum wider than long (nasus included); nasus well developed, tongue-like, slightly pointed anteriorly, slightly waisted, meeting body of scutum at approximately right angles; anterolateral angles slightly obtuse, rounded; lateral borders slightly convex; posterolateral angles obtuse, rounded;

posterior borders sinuous; posterior angle obtuse, rounded. Scutalae narrow, tapering, slightly blunted at tip, with pointed, outstanding setules. Sensillary setae with 8-10 setules in distal half. Sensillary sockets level with PL scutalae bases and set slightly obliquely. Shield lightly porose, with two larger pits near each PL angle.

Standard and other data of scutum and legs of the type series as in Table 1.

Eyes oval, conjoined, posterolateral to dorsal scutum; anterior eye with maximum diameter 16, posterior 11.

Dorsal idiosomalae normal, lightly tapering, slightly blunted at tip, moderately setulose, arranged 2 ("humeralis"), then 6, then in vague rows across dorsum; total about 55.

Ventral surface of idiosoma with a pair of pointed, setulose setae, 33 long, with centres of bases 34 apart, between coxae III. Behind coxae III opisthosoma with 42 setae, curved, setulose, pointed, but the more posterior setae longer, slightly blunted, resembling posterior dorsal idiosomalae. Anus 24 long by 13 across; 16 setae anterior to level of middle of anus, and 26 posterior. Urtigema well chitinized, oval, 25 long by 16 wide.

Coxalae 2, I, I, I, long, well setulose, tapering, pointed. Lateral coxala I 64 long, medial coxala I 68, coxala II 53, coxala III 46.

Dorsal tracheal opening present between posterolateral edge of gnathosoma and anterior border of coxa I (or overlying latter).

Dorsal tracheal opening present between posterolateral edge of gnathosoma and anterior border of coxa I (or overlying latter).

Gnathosoma normal; Combined chelicerae bases c. 73 across, by 91 long from tip of cheliceral fangs to posterior edge of cheliceral bases. Fangs stout, curved, blunt-pointed, with 3-5 strong retrorse teeth along concave (flexor, dorsal) edge, and 5-7 blunted denticles along convex (extensor, ventral) edge. Galeala 26 long, simple.

Palpi normal, palpal setal formula B, B, BNN, So + 7II. Palpal tibial claw three-pronged. No supracoaxala to gnathosoma or legs.

Description of legs of larva (from ACB520BA2 and ACB270A,B): Leg lengths (including coxae and claws): I 425, II 355, III 425. Scobular formulae: trochanters I, I, I; femora 6, 5, 4; genua 4, 4, 4; tibiae 8, 6, 6 (including 2 mastalae on tibia III); tarsi 26, 16, 13 (including one mastala on III). Leg specialized setae as follows: Leg I (from ACB520BA2): SoGel.38ad(21 long), VsGel.66pd(4), SoGel.71pd(22), SoTil.59d(16), VsTil.88d(2), SoTil.95ad(10) (i.e. slightly distal to Vs). Leg II (from ACB270A): SoGel.1.34pd(20), VsGel.64pd(1), SoTil.42pd(16), SoTil.89pd(10). Leg III (from ACB270B): SoGel.1.26pd(21), SoTil.1.50pd(27).

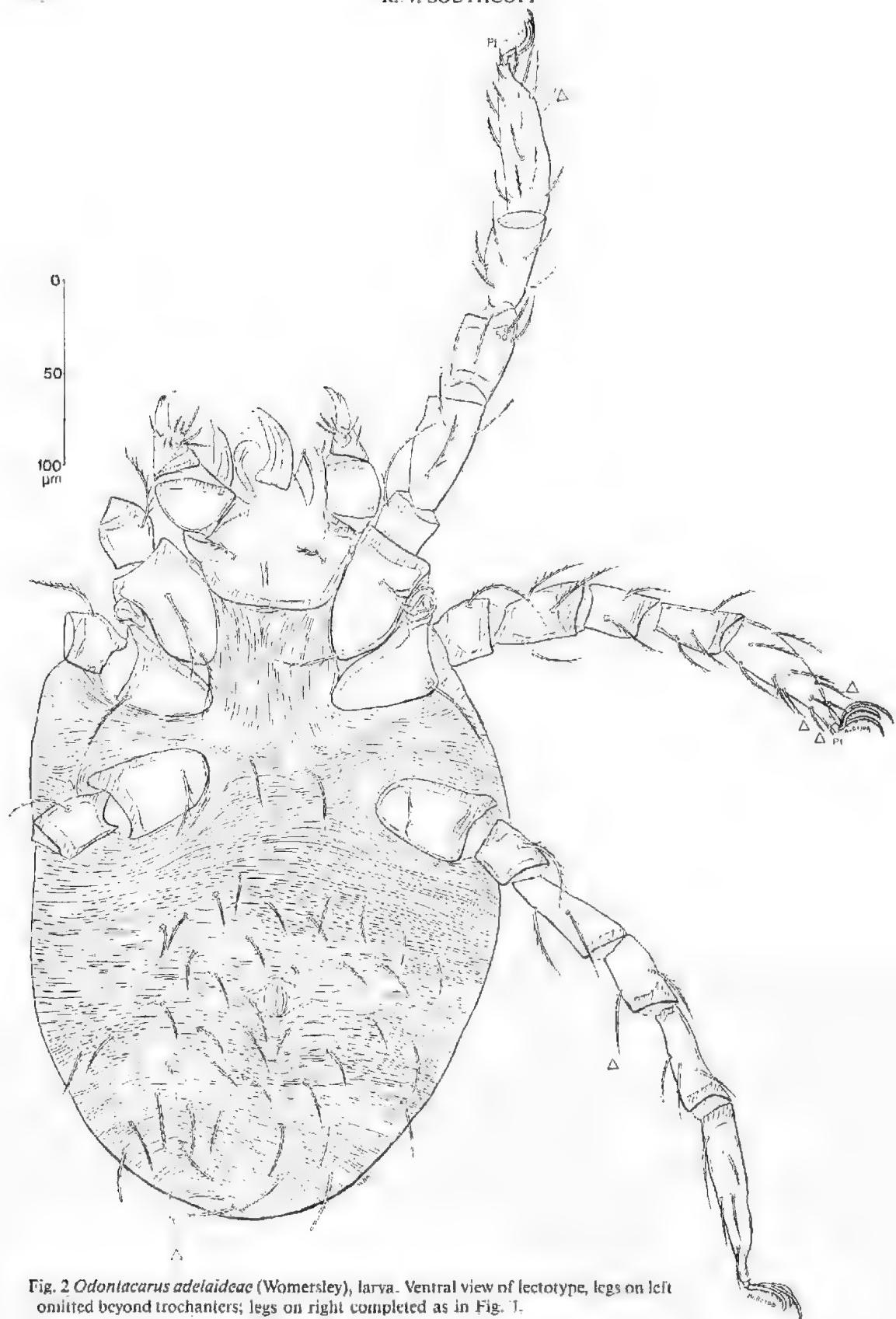


Fig. 2 *Odontacarus adelaideae* (Womersley), larva. Ventral view of lectotype, legs on left omitted beyond trochanters; legs on right completed as in Fig. 1.

TABLE I. Metric data for type series of *Odontacarus adelaideae* (Womersley) larvae

Character	N198831 (ACB67) Lectotype	n	mean	s.d.	Observed range
AW	66	5	70.80	±3.56	(66-74)
PW	84	5	87.80	±2.77	(84-91)
SB	24	5	28.20	±3.03	(24-32)
ASB	50	5	51.00	±1.73	(50-54)
PSB	28	5	29.80	±1.79	(28-32)
L	78	5	80.80	±3.35	(78-86)
LA	16	5	16.80	±1.10	(16-18)
LB	62	5	64.00	±2.83	(62-68)
LN	27	5	25.40	±2.30	(22-28)
W	96	5	95.60	±0.55	(95-96)
AP	28	5	30.40	±1.82	(28-32)
AM	36	5	37.20	±1.64	(36-40)
AL	36	5	35.80	±0.45	(35-36)
PL	49	4	53.25	±5.44	(49-61)
PL/AL	1.36	4	1.478	±0.15	(1.36-1.69)
AMB	11	5	10.60	±1.67	(9-13)
Sens:	55	3	53.67	±3.21	(50-56)
PW/LB	1.35	5	1.374	±0.08	(1.28-1.47)
DS	28-55	4	55.50 ²	±1.00	(55-57) ²
Hum ¹	55	4	55.50 ²	±1.00	(55-57) ²
MDS	28-31	5	32.80 ²	±1.30	(31-34) ²
PDS	34-39	5	40.60 ²	±3.13	(38-46) ²
GeI	57	4	56.75	±1.26	(55-58)
TiI	60	3	62.00	±2.00	(60-64)
Tai(L)	94	2	95.50	±2.12	(94-97)
Tai(H)	27	2	29.00	±2.83	(27-31)
Gell	44	5	47.40	±2.30	(44-50)
TiII	50	5	54.00	±2.35	(50-56)
TaiI(L)	78	5	84.00	±3.46	(78-86)
TaiI(H)	27	5	27.00	±0.71	(26-28)
GellII	51	2	53.00	±2.83	(51-55)
TiIII	68	2	70.50	±3.54	(68-73)
TaiII(L)	95	2	101.50	±9.19	(95-108)
TaiII(H)	24	2	23.00	±1.41	(22-24)
AW/AP	2.36	5	2.334	±0.14	(2.13-2.52)
AW/TiIII	0.97	2	0.985	±0.02	(0.97-1.00)
PW/TiIII	1.24	2	1.215	±0.04	(1.19-1.24)
PSB/SB	1.17	5	1.066	±0.12	(0.93-1.19)

¹ Humeral seta length² For maximum values

Both tarsi I and II bear a large central dorsal solenoidala: SoTaI.43d(15) and FaTaI.40ad(3) (from ACB270A); on tarsus II (from ACB270B) is SoTaII.40d(15), and FaTaII.37ad(4) (i.e. slightly proximal and anterior to SoTaII (in usual convention of legs being considered stretched out horizontally at right angles to main longitudinal axis of mite). Pretarsal formula 1, 1, 0. Tarsal claws normal, slender, falciform, simple, nonmedian longer than anterior and posterior, each with a fringe of minute onychotrichs.

Description of Protonymph: (Fig. 3) from mounted specimen ACB522BA5) Colour in life not observed, presumably orange-red. Shape irregularly spheroidal, 630 long, maximum width 430. Skin without setae, thin, more or less smooth but with many minor creases, possibly artefacts of mounting.

Developing limbs represented by finger-like processes; those of chelicerae and palpi still adnate to main mass of protonymph, those of legs becoming free.

A few setae and a few fragments of larval tracheae adhering to protonymphal skin.

Description of Deutonymph: (Figs 4-6) (from slide-mounted specimen ACB522AA/DI, supplemented by other specimens) Colour in life orange. Idiosoma ovoid, more pointed anteriorly and posteriorly, not waisted, flattened below; no division between propodosoma and metapodosoma. Propodosoma more or less conical; posterior pole of idiosoma rounded. Length of idiosoma (from tip of sagitta) 512, width 370; over-all length from chelicerae tips to posterior pole of idiosoma 634.

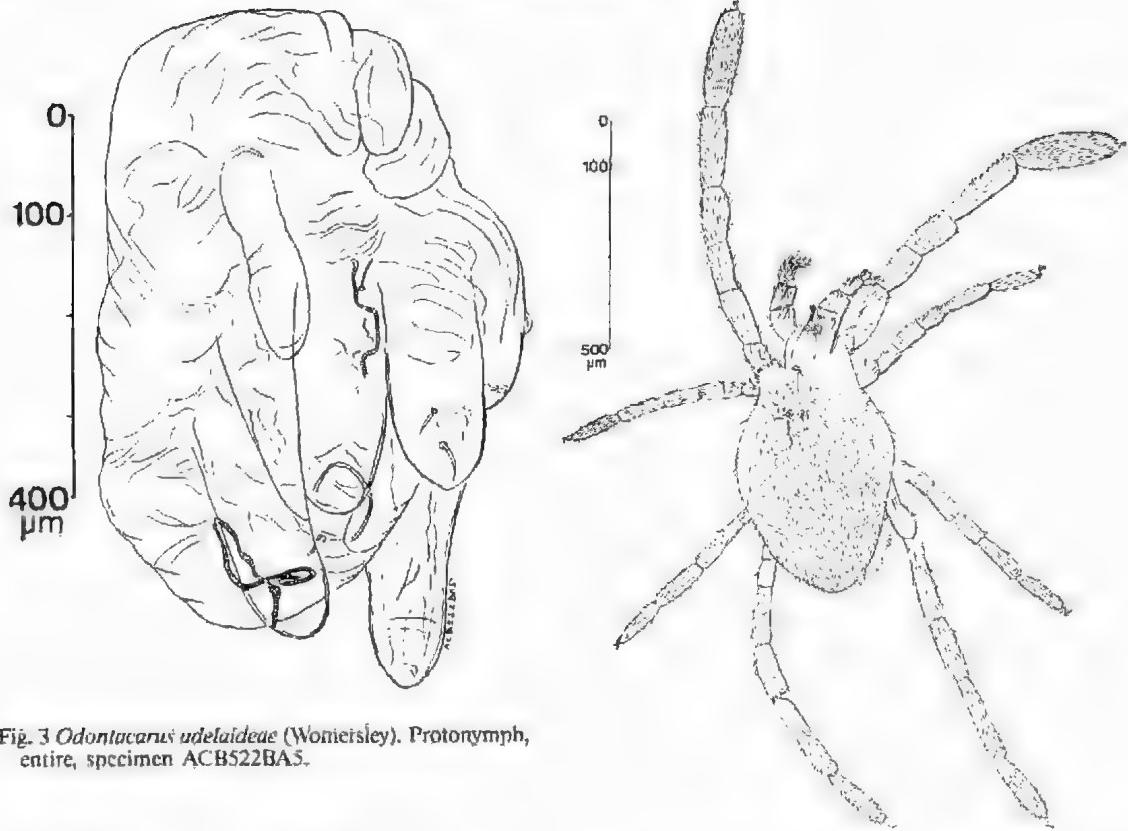


Fig. 3 *Odontocarus adelaideae* (Womersley). Protonymph, entire, specimen ACB522BA5.

Propodosoma bearing dorsally a short crista 151 long, with sagitta about 15 across, carrying two almost nude pointed setae 41 long. Sensillary area 46 across, with two large sensilla, each with a filiform sensillary seta 100 long, with faint setules in distal half. Crista produced posteriorad beyond sensilla, tapering to a blunt point 47 behind level of sensillary centres.

Crista surrounded by normal setae similar to those of whole of dorsum of idiosoma. Dorsal idiosomal setae unexpanded, pointed, lightly setulose, curved, 18–46 long, the posterior setae the longer. There is no clear separation into morphologically different types of setae in any area of the dorsum.

Ventral surface of idiosoma thickly covered with pointed, setulose setae, 15–34 long; setules more prominent than for dorsal setae; setae less setulose but longer towards posterior pole, where they are similar to the posterior dorsal idiosomal setae.

Genital aperture 86 long, by 50 wide; valves lightly chitinized; each medial valve with two or three setae 13–18 long at about mid-area, slender and less setulose than surrounding setae. Anus 49 long by 31 wide, with 2 or 3 curved setulose setae along each lateral valve, similar to surrounding setae.

Fig. 4 *Odontocarus adelaideae* (Womersley), Deutonymph, entire, dorsal aspect, specimen ACB521AA/DI.

Legs long, fairly thin; femoral to tibial segments more or less cylindrical. Lengths (including coxae and claws) I 960, II 570, III 595, IV 925; Leg scobulae pointed, setulose; interspersed among them are many pointed sensory setae (spinalae). A small vestigial, 5–6 long, present on each of tibia I and genua I and II, distally and dorsolaterally. Tarsus I outline and elongate oval, other tarsi more cylindrical (see fig. 4).

Other morphometric data as in Table 2.

Palpi normal, with generally lightly setulose setae (many appearing almost nude), but along dorsal (extensor) edges of segments a number of unilaterally setulose setae (pectinalae). Palpal tibial claw stout, blunted, with four accessory thickened setae on dorso-medial aspect. Palpal tarsus clavate, ovoid, with several setulose setae, but carrying also a cluster of terminal smooth sensory setae.

Cheliceral fangs fairly robust, curved, blunt-pointed, with a row of about 10 minute denticles along flexor (concave) edge.



Fig. 5 *Odontocarus adelaideae* (Womersley). Deutonymph: gnathosoma and adjacent structures, dorsal aspect (partly in transparency), from specimen ACB521AA/DI.

TABLE 2. Morphometric data for deutonymphs of *Odontacarus adelaideae* (Womersley).

Character	Specimen ACBS22AA/DI	n	mean	s.d.	Observed range
CL	104	8	115.38	±12.71	(95–135)
SB	25	9	26.56	±3.61	(20–31)
PDS	33–46	9	47.78	±3.83 ²	(44–56) ²
Gel	135	9	141.11	±14.00	(118–160)
Til	187	9	206.11	±20.33	(178–226)
Tal(L) ³	244	9	246.67	±18.26	(218–273)
Tal(H)	67	9	68.56	±4.45	(60–75)
GelII	75	8	79.63	±5.58	(72–86)
TilII	110	9	113.00	±10.51	(96–128)
TalII(L) ³	124	9	12.78	±13.27	(111–148)
TalII(H)	29	9	30.00	±3.43	(24–35)
GelIII	77	7	86.86	±8.11	(77–100)
TilIII	118	8	129.88	±13.66	(111–146)
TalIII(L) ³	117	8	127.38	±11.33	(114–143)
TalIII(H)	31	8	29.38	±3.78	(25–34)
GelIV	146	8	154.50	±11.65	(137–172)
TilIV	198	8	219.63	±24.23	(188–253)
TalIV(L) ³	175	8	182.00	±14.79	(162–205)
TalIV(H)	36	8	34.50	±4.17	(29–41)
Tal(L)/Til	1.30	9	1.23	±0.056	(1.15–1.30)

¹ CL = cristal length, measured from anterior tip of sagitta to level of midpoints of sensillary sockets² For maximum values³ Omitting claws and pedicle.

Identification of larvae of *Odontacarus (Leogonius)* in Australia

Comments

The recording of about 42 ventral opisthosomal setae in *O. adelaideae* larva invalidates caption number 12 of my earlier key to the larvae (Southcott 1986a pp. 179–180), which was based largely on previously published descriptions.

Accordingly, captions 12–14 should be replaced by the following:

- 12 More than 45 ventral opisthosomal setae present 13
- less than 45 (about 42) ventral opisthosomal setae present, AL setulae in range 33–40 µm long, PDS 34–46 µm long *O. adelaideae* (Womersley)
- 13 More than 75 dorsal idiosomal setae present *O. australiensis* (Hirst) (including *O. hirsti* (Womersley, 1944)²)
- Less than 70 dorsal idiosomal setae present 14
- 14 PL/AL < 1.20 *O. novaguinea* (Womersley, 1944)³ (including *O. longipes* (Womersley, 1945)³)
- PL/AL > 1.20 15

Key to deutonymph instars of *Leogonius* (Australia-SW Pacific area)

- 1 Dorsal idiosomalae arising from small platelets and about 25 µm long¹
- *O. novaguinea* (Womersley, 1944)
- Dorsal idiosomalae without the above combination of characters 2
- 2 Posterior dorsal idiosomalae over 50 µm long, Tal/Til mean 1.54 (tarsus I 210–228 µm long, tibia I 130–154 µm)²
- *O. australiensis* (Hirst, 1925) (syn. *O. hirsti* (Womersley, 1944)^{2,3})
- Posterior dorsal idiosomalae generally less than 50 µm long 3
- 3 Tarsus I longer than 300 µm (tarsus I 450 µm, tibia I 450 µm, Tal/Til = 1.00, dorsal idiosomalae to 30 µm long)¹ *O. longipes* (Womersley, 1945)
- Tarsus I less than 300 µm long 4
- 4 Posterior dorsal idiosomalae 15–20 µm long, Tal/Til 1.36 (tarsus I 185 µm long, tibia I 136 µm)⁴
- *O. audyi* (Radford, 1946)
- Posterior dorsal idiosomalae generally to about 45 µm long, Tal(L)/Til 1.15–1.30 (tarsus I 218–273 µm long, tibia I 178–226 µm) *O. adelaideae* (Womersley, 1944)

¹ From Goff (1979).² Synonymized by Domrow (1956) and Goff (1979).³ These two species (as larvae) were synonymized by Goff (1979). However, see the comment of Southcott (1986a, p. 191).¹ Womersley (1945).² Domrow (1956).³ Goff (1979).⁴ Nadchatram (1963).

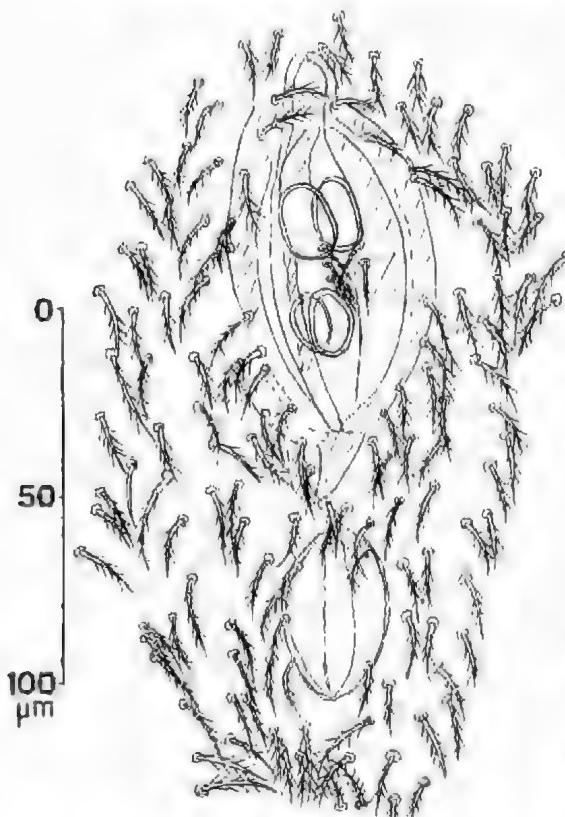


Fig. 6 *Odontocarus adelaideae* (Womersley). Deutonymph, external genitalia and anus. from specimen ACB521AA/DI.

Material examined of *Odontocarus adelaideae*: Type series: South Australia: Glen Osmond, Nov. 1931, D. C. Swan, from ears of cat, 3 paratypes (NI988333–NI988335, ACB941–943). Unley Park (not Unley, as stated by Womersley 1944), 1.ii.1941, R. V. Southcott, from ears of cat, one lectotype (NI988331, ACB67), one paratype (NI988332, ACB66).

The lectotype was designated as NI988331 because it has not been remounted since 1943 (indicated by my notes) and is, therefore, the most intact. Also it is in the same attitude as Womersley's (1944) figure.

I have excluded from the type series the three specimens recorded in the original description, from "Cairns, Queensland, 1939 W. G. H" [easlip], "from rats," as they can no longer be found in the collection of the South Australian Museum, and were presumably excluded by Womersley at some time after his 1944 paper. He did not refer to them in 1945, in his last publication on *Odontocarus*. Other material: S. Aust. Unley Park (all from ears of cats of topotype area, collected R.V.S.) 1.II.1941;

one specimen, ACB68; 9.II.1941, several specimens, ACB72, 74, 928; 1.III.1941, 3, ACB75–77; 11.III.1941, 2, ACB78, 79, 15.III.1941, 2, ACB80, 81; 29.III.1941, 1, ACB82; 30.III.1941, 1, ACB83; 4.IV.1941, 1, ACB84; 6.IV.1941, 1, ACB85; 11.IV.1941, 3, ACB86 B,C,E; 14.IV.1941, 1, ACB87; 16.XI.1941, 3, ACB100–102; 23.XI.1941, 5, ACB103; 29.XI.1941, 5, ACB104; 22.XII.1946, several, ACB270; 16.XII.1947, several, ACB319; 31.XII.1950, several, ACB520; 31.XII.1950, two batches of several larvae, from which deutonymphs were reared, ACB521, 522; 25.II.1951, several, ACB523; 1.III.1951, several, ACB524; 9.III.1951, 2, ACB525; 6.I.1952, several, ACB560 (deutonymphs reared).

Successful larva to nymph rearing experiments

Larvae were handled in the 1950–1952 series of experiments as stated above. One protonymph (ACB522BA5) was obtained, but the transformation was not observed, and discovered only when the tube was examined on 29.I.1951. Earlier examination on 14.I.1951 revealed nothing unusual (however in these wet tube studies observation is at times difficult).

Eleven deutonymphs were obtained from the 1950–1952 experiments. Nine of these came from experiments ACB521 and 522, with larvae collected on 31.XII.1950, and nymphs having emerged over 15–29.I.1951. With batch ACB560, collected on 6.I.1952, two newly emerged deutonymphs were found on 27.II.1952.

The finding of an intact protonymph was fortunate, as this instar is generally unrecognizable after the emergence of the deutonymphs.

From the above experiments, the larva to deutonymph transformations took 15–29 days. Domrow (1956) recorded that in *O. australiensis* deutonymphs took 25–28 days to emerge in his laboratory in Brisbane.

Transfer of larvae of *O. adelaideae* from cat to man

On the afternoon of 11 April 1941 I transferred seven attached larvae (batch ACB86) from the ears of a cat to the skin of the dorsum of my forearm, under a watchglass kept in place by sticking plaster. On removing the watchglass 2.5 hr later I found two small larvae attached to my skin. Removal of the watchglass periodically was necessary, as condensation made detailed observations impossible.

Next morning the underlying skin was sore. Three maculopapules with attached mites were observed at different sites; these maculopapules were 4–6 mm wide, and were itchy. That afternoon the area of erythema around the attachment sites had grown to 10–11 mm wide, these had become conjoined (only two mites were now attached). Small white specks were seen at the summits of the papules (four beneath one mite, three beneath the other).

presumably mite faeces. Small vesicles were present at the summit of each papule at the mite attachment sites (20–22 hours after initial attachments (codes as S + 20–22 hr)).

The itching, redness and vesiculation increased. The attached mites increased slowly in size to "half-grown". At S + 39 hr the whole area under the watchglass was itching, diffusely swollen and somewhat indurated; this area was 45 mm across, and by this stage the mites were considered full grown (as compared with the larvae that had been observed on the cat's ears). The papules had become so prominent as to press upon the covering watchglass. The mites continued to make small faecal pellets beneath them.

By S + c. 90 hr two vesicles had broken and were oozing serum. No lymphangitis or lymphadenopathy had developed.

After the mites had detached the swelling reduced rapidly, and scabs developed over the broken skin surfaces.

By S + 8 days the papules had regressed to being almost flat, and the erythema was fading. No general symptoms attributable to the mite bitings or their lesions developed.

Unfortunately, this attempt to obtain mite deutonymphs by human feedings was unsuccessful. A summarized account of this experiment was recorded earlier (Southcott, 1971).

Acknowledgments

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THE COMPOSITION AND DISTRIBUTION OF THE VEGETATION OF NORTH-WEST EYRE PENINSULA

BY F. TIVER, A. D. SPARROW & R. T. LANGE*

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The vegetation of inland north-western Eyre Peninsula, South Australia, is sampled for phytosociological analysis by transect quadratting. Using a combination of numerical classification (Bray-Curtis dissimilarity with average-linkage clustering) and ordination (detrended correspondence analysis), seven main vegetation associations are identified: *Eucalyptus dumosa-Westringia rigida*, *Eucalyptus gracilis-Stipa*, *Eucalyptus gracilis-Eucalyptus oleosa*, *Eucalyptus oleosa-Melaleuca pauperiflora*, *Eucalyptus oleosa-Enchylaena tomentosa*, *Eucalyptus brachycalyx* and *Eucalyptus yumbarrana-Triodia irritans*. The last occurs on the siliceous Moornaba sands, and the other six on the calcareous Woorinen Formation. Environmental parameters correlate only weakly with a floristic gradation over the calcareous soils, suggesting that historical influences may be important in determining the distributions of the vegetation types.

KEY WORDS: Eyre Peninsula, vegetation survey, vegetation analysis, classification, ordination, plant associations.

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Introduction

Until recently, the vegetation of north-western Eyre Peninsula remained relatively unknown. The first detailed study was that of Crocker (1946). Unfortunately the accompanying map only extends northwest as far as Poochera, where the vegetation is described as *Eucalyptus oleosa* – *E. gracilis* – *E. dumosa* edaphic complex. Specht (1972) also included only the southern-most portion of the area in his maps, describing the vegetation south of the Eyre Highway as *Eucalyptus socialis* – *E. gracilis* open scrub and that north of it as *Eucalyptus incrassata* – *Melaleuca uncinata* open scrub. Boomsma & Lewis (1980) described 16 communities, defined by the tall dominants, which occur on north-west Eyre Peninsula. Their distribution maps are not detailed enough to be able to extract the relative importance of any of these communities.

Descriptive surveys such as those mentioned above are not always capable of repetition by others (Nilsson 1986). For this reason, most modern surveys use quantitative data of the whole flora, and various forms of computer-assisted multivariate analysis, which result in a higher degree of objectivity and repeatability. A numerical classification of the vegetation of western Eyre Peninsula, one of the few such studies in South Australia, was undertaken by Margules & Nicholls (1987). Using complete species data from 104 plots each of 0.1 ha, cluster analysis was used to identify six vegetation communities on western Eyre Peninsula. This survey did not extend northwards

onto the sand dune formations. Statistical models were constructed to relate the occurrence of the six communities to three environmental variables: depth of carbonate layer, distance from the coast and latitude. Although allowing prediction of likely vegetation types in other remnant patches, these factors do not adequately describe the environmental factors important in determining the vegetation pattern.

The aims of this study were to classify the vegetation of north-western Eyre Peninsula (Fig. 1) using repeatable, numerical methods, and to provide some explanation of the main factors controlling the vegetation pattern.

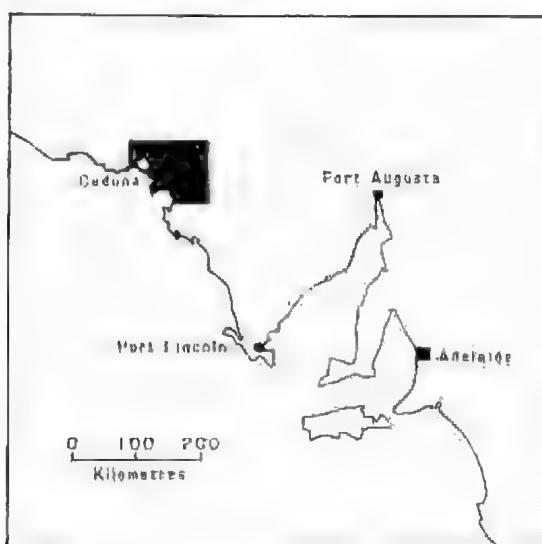


Fig. 1. Showing the location of the study area on north-western Eyre Peninsula, S.Aust.

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Geology, Landform and Soils of the Study Area

Most of the surface geological formations of western Eyre Peninsula (see Fig. 2) are derived from calcareous sands. It has been suggested that these sands were blown in from the exposed marine continental shelf during periods of low sea level and aridity, which occurred during the Pleistocene ice ages (Crocker 1946; Twidale & Campbell 1985). Another possibility is that the sands represent palaeo-dune systems that were formed by wave and wind action during periods of high relative sea level (Short *et al.* 1986).

The Bridgewater Limestone is composed of calcarenite, grains of calcareous sand cemented together with calcite crystals. In the maritime zone it is exposed as coastal cliffs but is otherwise covered by unconsolidated, deep, calcareous shelly sand of low water-holding capacity (Wright 1985). The Bakara Calcrete consists of calcarenite in which the shell fragments have been progressively dissolved and replaced by nodular and platy calcrete. To reduce the ecological complexity of the survey, these coastal limestone formations were excluded from the study.

The Woorinen Formation closely corresponds to the Chandada Plain landform in which the dunes have consolidated to form an undulating plain with

no surface drainage (Twidale & Campbell 1985). Calcrete is usually present as a bed of nodules beneath the surface. The soils are calcareous throughout, and range in texture from sands to clay loams. They are usually shallow and reddish brown, but sandier grey varieties and redder varieties with higher clay content have been reported; they have been extensively cleared for agriculture (Wright 1985). Areas of the calcareous sands normally associated with the Bridgewater Limestone also occur on the Woorinen Formation. Near the coast these sands are coarse and shelly, but further inland they are firmer with less-apparent shell fragments. Wright (1985) reports deficiencies in a wide range of minerals in these sands.

The Molineaux or Moornaba Sand is of extremely recent origin (c. 10 000 years b.p. onwards) and composed of sand dunes aligned in a NW-SE direction. Bleached white siliceous sands with a yellowish B horizon occur on the dunes. The underlying soils of the inter-dune corridors contain calcareous earths typical of the Woorinen Formation.

Methods

Sampling Strategy

A system of transects was chosen as the best compromise between equal coverage of the region



Fig. 2 The study area, showing major surface geological formations (after Blisser 1969).

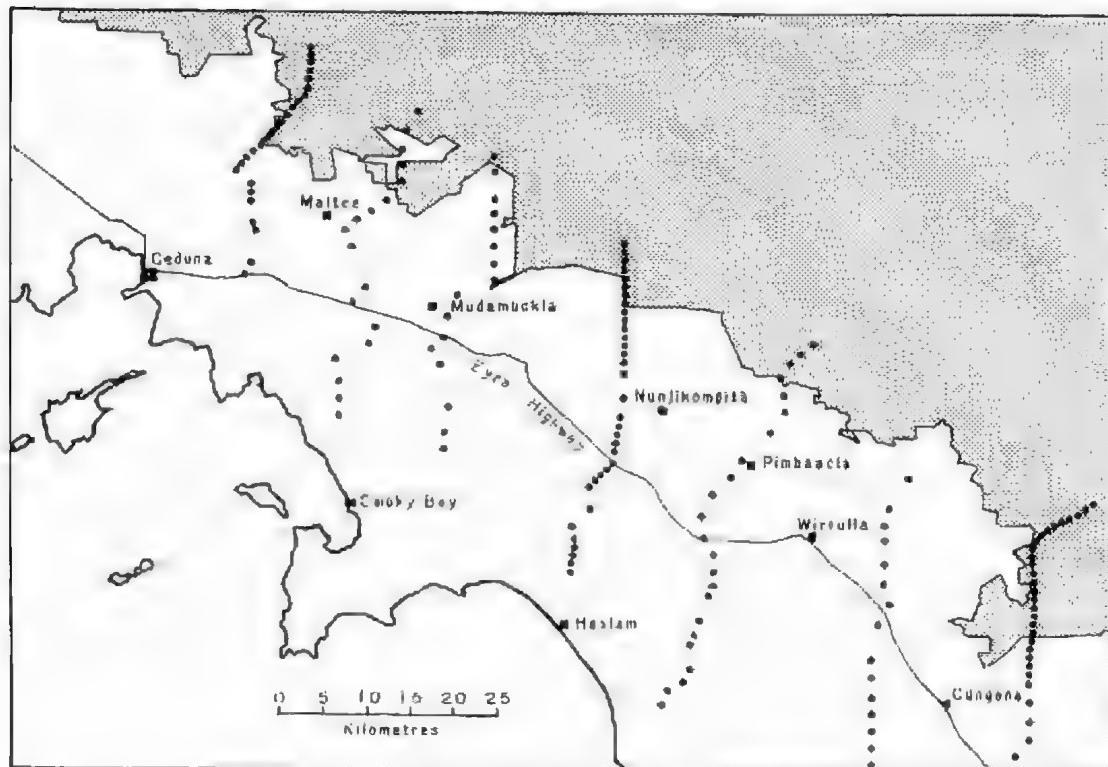


Fig. 3 The study area, showing location of sites along seven transects. Shading represents uncleared vegetation.

and efficiency of time spent on data collection. Transects were placed in suitable areas of native vegetation, running north and south from Ceduna, Maltee, Mudamuckla, Nunjikompita, Pimbaacla, Wirrulla and Cungena (Fig. 3). Transects were extended southwards only as far as the boundaries of the Bridgewater formation and its overlying coastal sands, and northwards as far as was accessible by four-wheel-drive vehicle. In the northern part of the study area, sites were placed 1 km apart, but in the southern part of the area, which is widely cleared for agriculture, native vegetation was often restricted to roadside remnants, and some sites had to be located as much as 2 km apart.

Field experience showed that quadrats of 0.1 ha as recommended by Whittaker (1978) and used by Margules & Nicholls (1987) were an appropriate size to achieve a good representation of species present without overlapping different vegetation types. One 50 x 20 m rectangular quadrat was measured at each site.

Vegetation Data

In each of the 162 sites sampled, all seed-plant species were recorded, although only native perennials were used for analysis. Annual species

were excluded because their occurrence depends on recent seasonal events; their inclusion would therefore lower the repeatability of the results. Introduced species were also excluded, since they do not form part of the natural vegetation pattern.

Total cover was estimated for each species present, and expressed as a semi-quantitative score, an adaption of the cover scale as Braun-Blanquet (1932); see Table 1.

Environmental Data

Anticipating some influence on floristic composition by various disturbance factors, disturbance by erosion, grazing, animal tracks, undergrowth clearance and earthworks was visually assessed on a scale ranging from 0 (nil) to 4 (severe). Sixty-two sites rated 2 (mild) or greater were excluded from analyses for definition of vegetation types.

Landform was assessed in the field as dune-crest, dune-flank, rise or plain (including wide interdune corridors). A soil core was dug in the centre of each quadrat and the depth to limestone recorded, in intervals of 10 cm. Texture was determined using the field method described by Northcote (1971). Existing rainfall maps were not detailed enough for the purposes of this study, so a rainfall map was

constructed, using complete Bureau of Meteorology rainfall records for 24 recording stations within or near the study area. This enabled the average rainfall at each site to be estimated and classed into 12 mm intervals.

Vegetation Analysis

The need to classify vegetation raises the question of whether vegetation types occur as discrete entities with distinct boundaries, or whether classifications are merely abstractions imposed by ecologists onto a continuously variable vegetation (Greig-Smith 1983). If vegetation consisted of random combinations of species a continuum would result and classification into discrete groups would be an entirely arbitrary process. If, on the other hand, variation was always discontinuous and no intergradation occurred, there would be a finite number of vegetation types in existence, and classification would be a simple matter. The actual case lies between these two extremes, ranging from the near discontinuous and distinct vegetation types to almost continuous ecotones (Webb 1954).

Consequently, a combination of two complementary analysis techniques is recommended when investigating vegetation patterns; a classification to define vegetation types, and an ordination to examine the relationships between the groups and the extent of ecotonal behaviour between them (Gauch 1982).

For classification purposes, the dissimilarity between all pairs of sites was calculated with the Bray-Curtis distance coefficient, and then sites

TABLE I. Semi-quantitative scores expressing percentage cover (adapted from Braun-Blanquet 1932).

Cover Score	Percentage Cover
0	absent
1	0 - 1
2	1 - 2
3	2 - 10
4	10 - 50
5	50 - 100

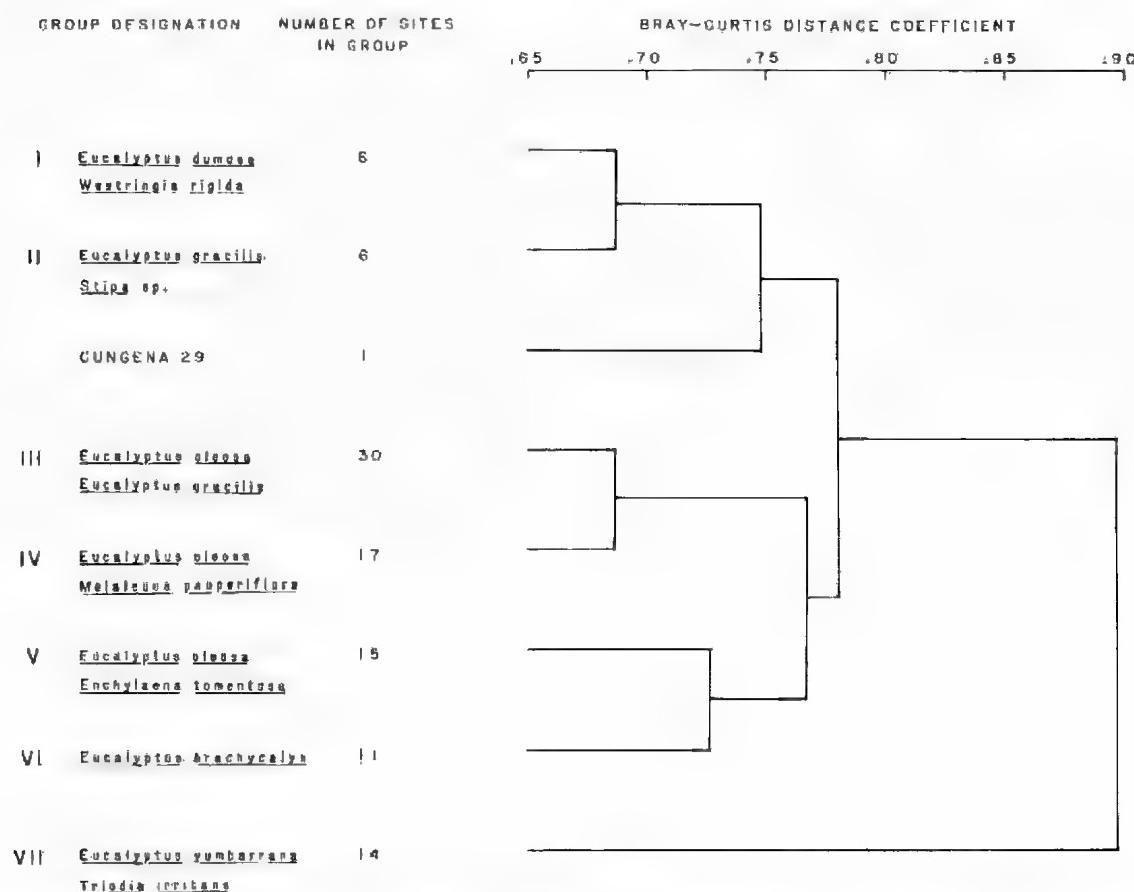


Fig. 4 Summary of dendrogram from clustering analysis showing arrangement of groups at 0.65 distance level.

grouped from the least to the most dissimilar by the unweighted pair group method using arithmetic averages (UPGMA; Legendre & Legendre 1983) to produce a hierarchical dendrogram, the branches of which represent vegetation types. The complementary ordination method chosen was detrended correspondence analysis, DCA (Gauch 1982). Ordination methods such as DCA rank sites along a series of axes which describe the major floristic variation. The results are displayed as a scattergram from which continuity and disjunction of vegetation types can be determined and with which environmental factors can be correlated. The numerical taxonomy computer software package NTP (Belbin *et al.* 1984) was used for both analyses.

For the purpose of preparing vegetation maps, the sixty-two disturbed sites were returned to the data set, and a further cluster analysis performed. By the proximity of these sites on the dendrogram to sites of known vegetation type, most of the remaining sites were identified as belonging to one of the major vegetation types.

Results

The classification dendrogram is summarised in Fig. 4. Field notes indicated that the groupings defined at the 0.65 distance level were the most readily interpreted, a higher level producing groups with large internal variation, and a lower level producing too many groups for consideration. Seven major vegetation types were identified at the 0.65 level, one of which, type VII, was widely

dissimilar from the other groups, only fusing with them at 0.90 level. A minor vegetation type was also identified. Represented by only one site, Cungena 29, this site was dominated by *Callitris preissii*, rather than a eucalypt species.

The relationships between the vegetation types can be seen from the ordination; a plot of the first two ordination axes is given in Fig. 5. The first axis explained 50% of the variation in the data set, and corresponds to the first major branching of the dendrogram, separating vegetation type VII from the others. The separation between the remaining six communities is largely supported by the ordination, although there is a certain degree of overlap, most marked between types I and II, and types V and VI. The relationship of these six vegetation types to each other obviously tends towards the "ecotone" rather than the distinct "association" end of the scale in vegetation pattern as described by Webb (1954).

The species consistent in each of the vegetation types are presented in Table 2 and Fig. 6 summarises the associated landforms, soils and rainfall. Table 3 gives a full listing of species found in the seven vegetation types. Understorey species are equally important as shrubs and trees in delineating vegetation type.

The vegetation types, their distributions (Fig. 7) and their environmental correlates are discussed below. The types have been named "associations" according to usual ecological practice, even though they do not fully fit the formal definition of "association" given by Braun-Blanquet (1932).

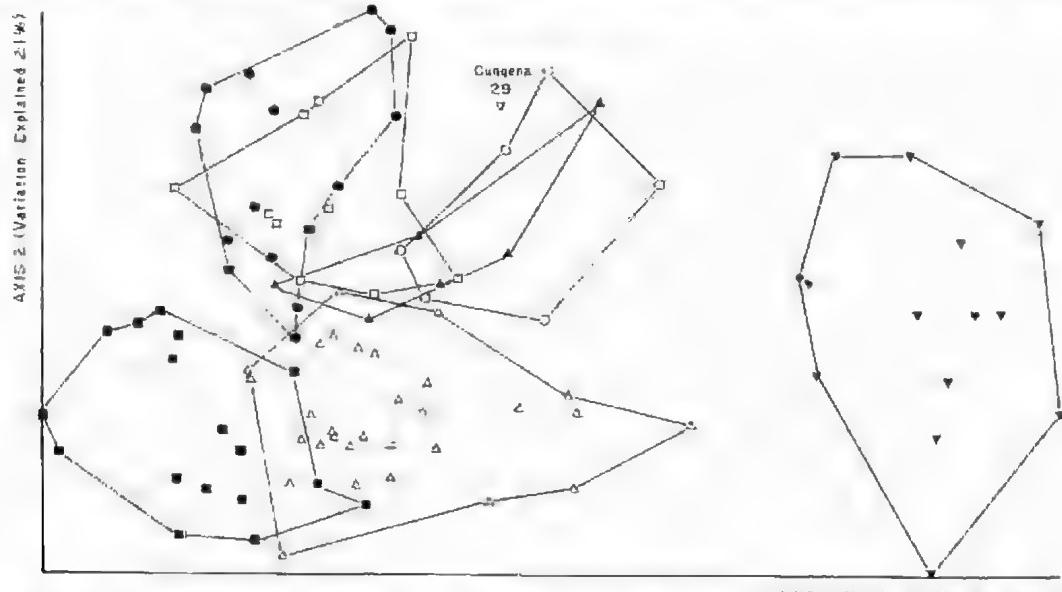


Fig. 5 DCA ordination showing relationships between the seven major vegetation types. Symbols denoting vegetation type are as follows: O, I; ▲, II; Δ, III; ■, IV; ●, V; □, VI; ▼, VII.

TABLE 2. Plant species characteristic of the seven major vegetation types. Marked species had a cover score of two or greater when present, and could be considered dominants.

VEGETATION TYPE	CHARACTERISTIC PLANT SPECIES Key Species (75–100% of sites)	Usually Present (50–74% of sites)
I	<i>Cassinia nemophila</i> • <i>Eucalyptus dumosa</i> • <i>Geijera linearifolia</i> • <i>Westringia rigida</i> • <i>Acacia collieoides</i> <i>Eremophila glabra</i> <i>Melaleuca lanceolata</i> <i>Zygophyllum apiculatum</i>	<i>Eucalyptus gracilis</i> • <i>Eucalyptus oleosa</i> • <i>Dianella revoluta</i> <i>Exocarpus aphyllus</i> <i>Pittosporum phylliraeoides</i> <i>Rhagodia preissii</i>
II	<i>Eucalyptus gracilis</i> • <i>Stipa</i> sp. • <i>Enchytraea tomentosa</i> <i>Geijera linearifolia</i>	<i>Acacia collieoides</i> • <i>Eucalyptus oleosa</i> • <i>Eremophila glabra</i> <i>Melaleuca lanceolata</i> <i>Sclerolaena obliquicuspis</i>
III	<i>Eucalyptus gracilis</i> • <i>Eucalyptus oleosa</i> • <i>Westringia rigida</i> • <i>Zygophyllum aurantiacum</i>	<i>Eremophila scoparia</i> • <i>Triodia irritans</i> • <i>Maireana erioclada</i> <i>Rhagodia crassifolia</i>
IV	<i>Eucalyptus oleosa</i> • <i>Melaleuca pauperiflora</i> •	<i>Rhagodia crassifolia</i>
V	<i>Eucalyptus oleosa</i> • <i>Enchytraea tomentosa</i> • <i>Geijera linearifolia</i> <i>Zygophyllum aurantiacum</i>	<i>Maireana erioclada</i> • <i>Rhagodia crassifolia</i> • <i>Sclerolaena diacantha</i> <i>Sclerolaena obliquicuspis</i> <i>Threlkeldia diffusa</i>
VI	<i>Eucalyptus brachycalyx</i> • <i>Maireana erioclada</i> <i>Rhagodia crassifolia</i>	<i>Melaleuca pauperiflora</i> • <i>Enchytraea tomentosa</i> <i>Sclerolaena diacantha</i> <i>Threlkeldia diffusa</i> <i>Zygophyllum aurantiacum</i>
VII	<i>Eucalyptus yumbarrana</i> • <i>Melaleuca eleuthrosiachya</i> • <i>Triodia irritans</i> •	<i>Dianella revoluta</i> <i>Eremophila crassifolia</i> <i>Podolpis capillaris</i>

The Vegetation Associations

Association I: *Eucalyptus dumosa*-*Westringia rigida*

The closest counterpart in the literature is the *Melaleuca lanceolata* association of Boomsma & Lewis (1972), which is said to occur with a number of species as co-dominants, including *Eucalyptus dumosa* and *E. gracilis*. Their classification includes a much wider range of vegetation associations than is here defined. It occupies a somewhat irregular distribution throughout the study area, restricted to rising ground on shallow calcrete, and the least sandy soils (sandy loams and loams).

Association II: *Eucalyptus gracilis*-*Stipa*

This vegetation association could be described as a depauperate variation of Association I. Although some of the same species are present, *Eucalyptus gracilis* is the most important tall species uniting the group. The lower diversity understorey

often includes a high percentage of perennial grass (*Stipa*). The relationship of Associations I and II is indicated by their proximity on the dendrogram (Fig. 4) and overlap on the ordination (Fig. 5).

The association has not been previously recorded on western Eyre Peninsula, and *E. gracilis* has only ever been reported as a co-dominant with other mallee species for the whole state (Boomsma & Lewis, 1980). Its distribution is also irregular, occurring on the dry central to northern section of the Cungnat transect, but also scattered through the southern Pimbaacla and Wirrulla transects at higher rainfall. Very shallow, light soils on low lying ground are consistent with its occurrence. The resulting harsh moisture conditions probably reduce the number of understorey species present to those which can tolerate them, such as the shallow-rooted *Stipa* and *Sclerolaena* spp.

Association III: Eucalyptus gracilis-oleosa

Association III probably forms the core of the *Eucalyptus oleosa* / *E. gracilis* association identified by Crocker (1946) and Specht (1972), although Specht appears to misidentify *E. oleosa* as *E. socotrana*. It is the most common vegetation association in the northern part of the study area, but was not recorded by Margules & Nicholls (1987).

Its occurrence in the southern section of the Nunjikompita transect at slightly higher rainfall seems to suggest that its distribution is more restricted by soil than climatic factors. It is not present in the south-western part of the study area because the calcareous sands there favour other vegetation associations such as IV and VI, or on the south-eastern section where calcrete outcrops favour Associations I and II.

The occasional occurrence of Association III on dune flanks may be explained by historical factors. It is the most common inter-dune vegetation of the northern part of the study area, occurring on medium depth to shallow soils. Since the Molineaux sands have been deposited over only the last few thousand years, they are relatively unstable. In some instances sand from these dunes has drifted on to calcareous earths in the interdunes already occupied by Association III vegetation, and the long-lived species such as *E. oleosa* and *E. gracilis* persist on a soil which would perhaps not at present favour their establishment. The understorey in these cases tends to include species less typical of the association, such as *Triodia irritans*.

Association IV: Eucalyptus oleosa-Melaleuca pauperiflora

Association IV contains a very species-poor and sparse understorey of chenopods such as *Rhagodia crassifolia* and *Maireana erioclada*. A known vegetation association including *Eucalyptus oleosa*, *Rhagodia crassifolia*, *Zygophyllum aurantium*, *Sclerolaena dioecantha* and *Melaleuca lanceolata* (Margules & Nicholls 1987), is probably equivalent to it, their *Melaleuca lanceolata* a possible misidentification of *M. pauperiflora*.

Association IV occurs mainly in the southwestern part of the study area, on shelly calcareous sands, with scattered occurrences in the north, for example, on the Nunjikompita transect, where outliers of this soil type occur on rises in the inter-dunes. These outliers are probably remnants of the old coastal dune environment which would have been present before the Molineaux sands were deposited. Although the vegetation association appears to occur at slightly higher rainfall, this may simply be a result of the soil type which favours its occurrence being characteristic of the southern coastal higher rainfall areas. The low diversity of the association may be an indication that only a

few understorey species are able to persist on the coarse shelly sands.

Association V: Eucalyptus oleosa-Enchylaena tomentosa

Vegetation falling within Association V is very variable and a large number of disturbed roadside sites were most closely allied to it, indicating that it may not be a naturally occurring association, but a result of disturbance. Many of the species are unpalatable, such as *Grevillea linearifolia*, or low growing chenopods, which suggests removal of more palatable understorey species by grazing. Further investigation would be required to ascertain if any of the sites represent a naturally occurring Association V.

Association VI: Eucalyptus brachycalyx

Vegetation Association VI includes *Eucalyptus brachycalyx* as the important upper-storey species, together with a range of low chenopods similar to that of Association V. The floristic similarity results in considerable overlap between these two associations on the ordination (Fig. 5). It is most common towards the coast, occurring in the southern central and western part of the study area on shallower soils than Association IV.

Association VII: Eucalyptus yumbarrana-Triodia irritans

It is probable that *Eucalyptus yumbarrana* was previously recorded as *Eucalyptus socialis*, and that the *E. socialis/Melaleuca uncinata* sandhill association of Specht (1972) corresponds to Association VII, as does Margules & Nicholls' Community I if their *Melaleuca adnata* is re-identified as *M. eleutheraestachya*.

Vegetation Association VII is restricted to the sand-dunes of the northern, low rainfall part of the study area. The species characterising it are entirely different from those found in the other vegetation associations, and include many species with distributions in higher rainfall parts of the state, such as *Lomandra leucocephala* and *Gahnia lanigera* (Jessop & Toelken 1986). This major floristic disjunction corresponds to a similar observation in north-western Victoria, where the most marked discontinuity of mallee vegetation was between a *Eucalyptus incrassata/Hibbertia Leptospermum* association with "southern temperate" affinities, and all the other associations, in which semi-succulent herbs, especially chenopods, were prominent (Noy-Meir 1971).

The disjunction observed is related to the geology, since the heavier soils of the exposed Woornin Formation present in the inter-dune corridors typically support vegetation of Associations I, II or III. The combined effect of coarse texture and

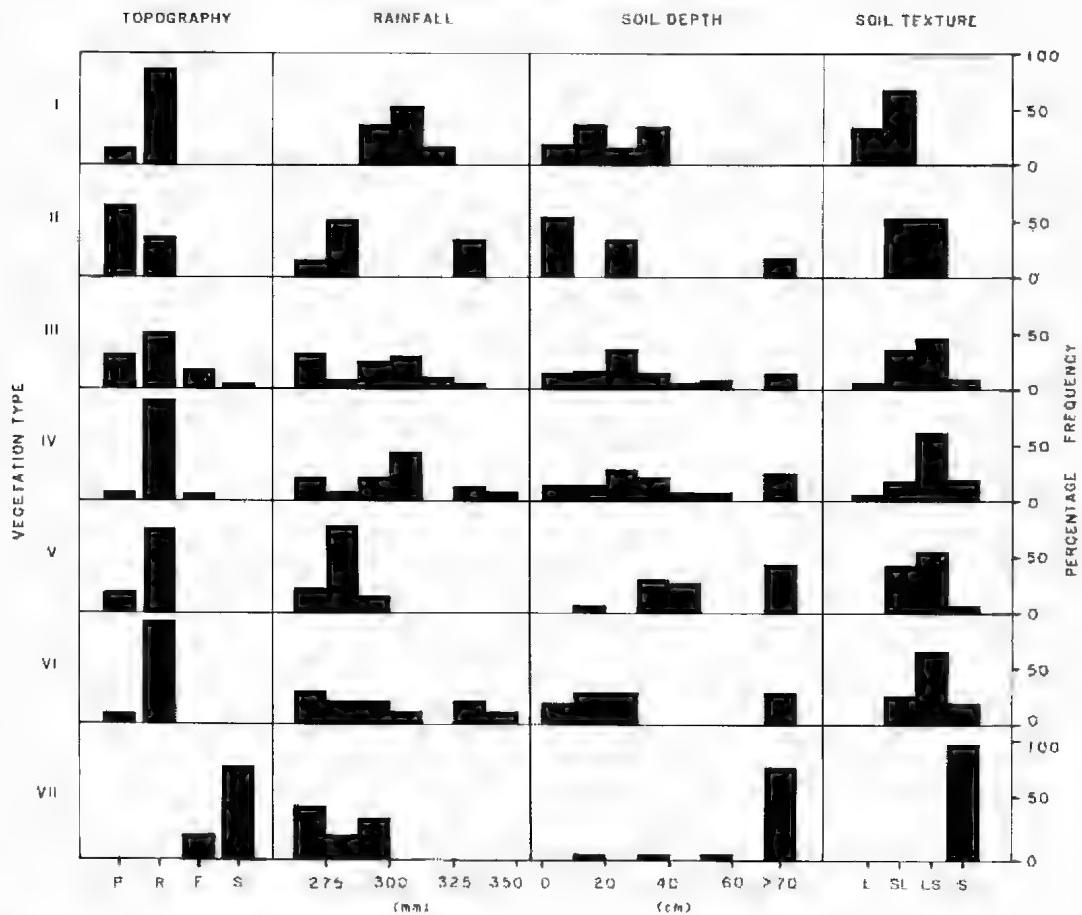


Fig 6. Histograms summarising observed environmental patterns for each of the vegetation types. For topography: P, plain; R, rise; F, dune flank; S, sandhill. For soil texture: L, loam; SL, sandy loam; LS, loamy sand; S, sand.

increased depth of the sands of the dunes presumably creates a more favourable water relations environment, which allows the presence of a suite of species normally requiring higher rainfall. There is a higher percolation rate and deeper penetration of rainfall into sands than into clays, while evaporation dries the surface soil to a similar depth regardless of texture, so that at the end of a long dry period, there would be more water available in the root zone of sandy soils than in clays (Walter & Stadelmann 1974). Clays also have a higher water holding capacity due to their smaller pore size (Ball 1986). This means that a larger amount of rainfall is required to bring air-dry clay to a range where water is available to plants than for sands.

Discussion

There is a clear vegetational discontinuity between the two predominating geological

formations of north-western Eyre Peninsula, the siliceous Moornaba sand dunes and the calcareous Woorinen soils. Although it is possible to recognise plant associations within the vegetation of the Woorinen Formation and to relate their distributions to environmental features in a general way, sharp discontinuities do not exist. The strong gradation of associations is typical of the mallee on Woorinen Formation and its equivalents across the whole of S. Aust. (Sparrow unpublished data).

There are two possible interpretations of these observations. Firstly, since there is no strong environmental discontinuity within the Woorinen Formation, the gradation may reflect combinations of species with independent environmental responses, which, further confounded by disturbance, results in almost continuous ecotones. Alternatively, the gradation of mallee associations could be caused by some degree of independence of the mallee and understorey strata. The mallees,

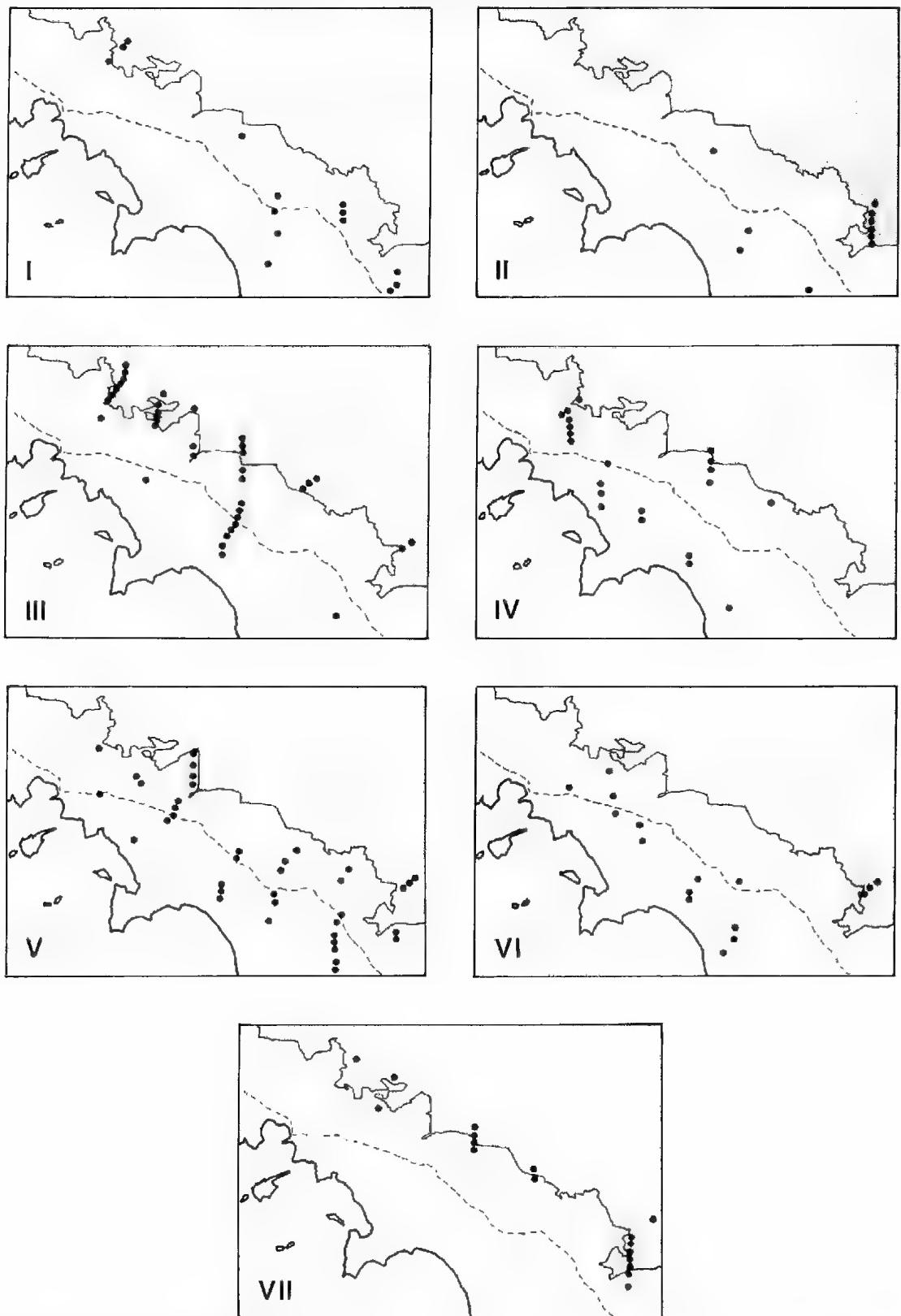


Fig. 7 Distribution maps of the seven major vegetation types. Shading represents uncleared vegetation and the broken line marks the Eye Highway.

TABLE 3: Full species list (nomenclature following Jessop & Toelken 1986) showing occurrence in the seven major vegetation types. Occurrence in sites that could not be assigned to a major vegetation type are grouped in the final column. Introduced species are indicated with an asterisk.

Species	Vegetation Type								Other
	I	II	III	IV	V	VI	VII	Other	
<i>Acacia calamifolia</i> Sweet ex Lindley	+	+	+	-	-	-	+	-	
<i>Acacia colletioides</i> Benth.	+	+	+	-	+	+	+	+	
<i>Acacia hakeoides</i> Cunn. ex Benth.	+	-	+	-	+	+	-	-	
<i>Acacia ligulata</i> Cunn. ex Benth.	+	-	-	-	-	-	+	+	
<i>Acacia merrallii</i> F. Muell.	+	+	+	+	+	+	+	+	
<i>Acacia notabilis</i> F. Muell.	+	-	-	-	-	-	-	-	
<i>Acacia oswaldii</i> F. Muell.	+	+	+	-	+	-	-	+	
<i>Acacia rigens</i> Cunn. ex Don	-	-	-	-	-	-	+	-	
<i>Acacia sclerophylla</i> Lindley	-	+	+	-	+	-	-	-	
<i>Acacia spinescens</i> Benth.	-	-	-	-	-	-	-	-	
<i>Alyxia buxifolia</i> R. Br.	-	-	-	-	+	-	-	-	
<i>Amyema melaleucae</i> (Miq.) Tieghem	-	-	-	-	-	-	-	-	
<i>Atriplex acutibractea</i> R. Anderson	+	+	+	+	+	+	+	+	
<i>Atriplex stipitata</i> Benth.	-	+	-	-	+	-	-	-	
<i>Atriplex vesicaria</i> Heward ex Benth.	-	+	+	+	+	-	-	-	
<i>Beyeria lechenaultii</i> (DC.) Baillon	+	-	-	-	-	-	-	-	
<i>Beyeria opaca</i> F. Muell.	-	-	-	+	+	-	-	-	
<i>Billardiera cymosa</i> F. Muell.	-	-	-	+	-	-	-	-	
<i>Boronia coerulescens</i> F. Muell.	-	-	-	-	-	-	-	-	
<i>Callitris preissii</i> ssp. <i>preissii</i> Miq.	-	+	-	-	-	-	-	-	
<i>Callitris preissii</i> ssp. <i>verrucosa</i> (Cunn. ex Endl.) J. Garden	-	-	-	-	-	-	-	+	
<i>Carpobrotus rossii</i> (Haw.) Schwantes	-	-	-	+	+	+	-	-	
* <i>Carrichtera annua</i> (L.) DC.	-	+	-	+	+	+	-	+	
<i>Cassia nemophila</i> var. <i>coriacea</i> (Benth.) Symon	+	+	+	-	+	-	-	+	
<i>Cassia nemophila</i> var. <i>nemophila</i> Cunn. ex J. Vogel	+	+	-	+	-	-	-	-	
<i>Cassia nemophila</i> var. <i>platypoda</i> (R. Br.) Benth.	+	+	-	+	+	-	+	+	
<i>Cassytha glabella</i> R. Br.	+	-	-	-	-	-	-	-	
<i>Cassytha melantha</i> R. Br.	+	-	+	+	+	+	+	-	
<i>Casuarina cristata</i> Miq.	-	-	-	-	+	-	-	+	
<i>Chenopodium desertorum</i> (J. Black) J. Black	-	-	-	-	-	-	-	-	
* <i>Cratystylis conocephala</i> (F. Muell.) S. Moore	-	-	0	-	+	+	-	-	

TABLE 3 cont. Full species list (nomenclature following Jessop & Toelken 1986) showing occurrence in the seven major vegetation types. Occurrence in sites that could not be assigned to a major vegetation type are grouped in the final column. Introduced species are indicated with an asterisk.

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Species	Vegetation Type								Other
	I	II	III	IV	V	VI	VII	Other	
<i>Grammosolen truncatus</i> (Ising) Haegi			+	-	-	-	-	+	-
<i>Grevillea huegelii</i> Meissner	+	+	+	+	+	-	-	-	-
<i>Hakea francisiana</i> Maconochie			-	-	-	-	+	-	-
<i>Halgania cyanea</i> Lindley	-	-	-	-	-	-	+	-	-
<i>Halgania lavandulacea</i> Endl.	-	-	-	-	-	-	+	-	-
<i>Helichrysum bilobum</i> Wakef.			-	-	-	-	+	-	-
<i>Hybanthus floribundus</i> (Lindley) F. Muell.	-		-	-			+	-	-
<i>Ixiolaena pluriseta</i> Haegi	-	-	-	-	-	-	+	-	-
<i>Lasiopetalum behrii</i> F. Muell.	-	-		-	-	-	+	-	-
<i>Lepidosperma laterale</i> R. Br.	-			-	-	-	+	-	-
<i>Leptospermum coriaceum</i> (F. Muell.) Cheel	-	-	-				+	-	-
<i>Leucopogon cordifolius</i> Lindley	-	-	-	-	-	-	+	-	-
<i>Logania nuda</i> F. Muell.	-	-					+	-	-
<i>Lomandra collina</i> (R. Br.) Ewart	-	-	-	-	-	-	+	-	-
<i>Lomandra effusa</i> (Lindley) Ewart	+				-	-	-	-	-
<i>Lomandra leucocephala</i> (R. Br.) Ewart	-	-	-	-			+	-	-
* <i>Lycium ferocissimum</i> Miers	-	-	-	+			+	-	-
<i>Maireana appressa</i> Paul G. Wilson	+	+	+	+	+	+	+	-	-
<i>Maireana brevifolia</i> (R. Br.) Paul G. Wilson	-			-	+	+	-	+	-
<i>Maireana enchytraenoides</i> (F. Muell.) Paul G. Wilson	-	+	-	-	-	-	-	-	-
<i>Maireana erioclada</i> (Benth.) Paul G. Wilson	-	-	-	-	+		-	-	-
<i>Maireana pentatropis</i> (Tate) Paul G. Wilson	+	+	-	+	+	-	-	-	-
<i>Maireana sedifolia</i> (F. Muell.) Paul G. Wilson	-	-	-	-	+	-	-	-	-
<i>Maireana trichoptera</i> (J. Black) Paul G. Wilson	+	-	+		+	-	+	-	-
<i>Melaleuca acuminata</i> F. Muell.	+	+	+	-	-	-	+	+	-
<i>Melaleuca eleutherostachya</i> F. Muell.	-	-	+				+	-	-
<i>Melaleuca lanceolata</i> Otto	+	+	+	-	+	+	+	-	-
<i>Melaleuca pauperiflora</i> F. Muell.	+		+	+	+	+	+	+	-
<i>Microcybe multiflora</i> Turcz.	-	-	+	-			-	-	-
<i>Muehlenbeckia gunnii</i> (Hook. f.) Walp.	+		-	-	-	-	+	-	-
<i>Myoporum platycarpum</i> R. Br.	+	-	-	+	+	-	-	-	+
<i>Olearia brachyphylla</i> (F. Muell. ex Sonder) Wakef.	+	+	-	-	+	-	-	-	-

TABLE 3 cont. Full species list (nomenclature following Jessop & Toelken 1986) showing occurrence in the seven major vegetation types. Occurrence in sites that could not be assigned to a major vegetation type are grouped in the final column. Introduced species are indicated with an asterisk.

Species	Vegetation Type								Other
	I	II	III	IV	V	VI	VII	Other	
<i>Olearia floribunda</i> (Hook. f.) Benth.	-	-	-	-	-	-	-	+	-
<i>Olearia magniflora</i> (F. Muell.) F. Muell. ex Benth.	+	+	+	+	+	+	-	-	-
<i>Olearia muelleri</i> (Sonder) Benth.	+	+	+	+	+	+	+	+	-
<i>Olearia pimelioides</i> (DC.) Benth.				-	-	-	+	-	
<i>Pimelea microcephala</i> R. Br.		-	-	-	+	-	-	-	
<i>Pittosporum phylliraeoides</i> DC.	+	+	+	-	+	+	+	+	+
<i>Podolepis capillaris</i> (Steetz) Diels	+	-	+	-	-	-	-	+	-
<i>Ptilotus obovatus</i> (Gaudich.) F. Muell.	+	-	-	-	-	-	-	-	-
<i>Ptilotus spathulatus</i> (R. Br.) Poiret	+	+	-	-	+	-	-	-	-
<i>Pultenaea elachista</i> (F. Muell.) Crisp	-	-	+	+	-	-	+	-	
<i>Rhagodia crassifolia</i> R. Br.	+	+	+	+	+	+	+	+	-
<i>Rhagodia parabolica</i> R. Br.		-	-	-	+	-	-	-	
<i>Rhagodia preissii</i> Miq.	+	+	+	+	+	+	+	+	+
<i>Rhagodia spinescens</i> var. <i>deltophylla</i> F. Muell.	+	+	-	-	+	-	-	-	-
* <i>Salsola kali</i> L.	+	-	+	+	+	-	-	-	+
<i>Santalum acuminatum</i> (R. Br.) A. DC.	+	+	+	+	+	+	+	+	-
<i>Scaevola bursariifolia</i> J. Black	-			+	+	-	-	-	-
<i>Scaevola spinescens</i> R. Br.	+	+	+	-	+	-	-	-	+
<i>Schoenus subaphyllus</i> Kük	-	-	-	-	-	-	-	+	-
<i>Sclerolaena diacantha</i> (Nees) Benth.	+	+	+	+	+	+	+	+	+
<i>Sclerolaena obliquicuspis</i> (R. Anderson) Ulbr.	+	+	+	+	+	+	+	-	+
<i>Sclerolaena uniflora</i> R. Br.	+	+	-	-	-	-	-	-	+
<i>Sida corrugata</i> Lindley	+	-	-	-	-	-	-	-	-
* <i>Solanum coactiliferum</i> J. Black	-	-	-	-	-	-	-	+	-
<i>Stelligera endecaspinus</i> A. J. Scott	-	-	+	-	-	+	+	+	-
<i>Stipa</i> spp. L.	+	+	+	+	+	+	+	+	+
<i>Templetonia battii</i> F. Muell.	-	-	-	-	+	-	-	-	-
<i>Threlkeldia diffusa</i> R. Br.	+	+	+	+	+	+	+	-	-
<i>Triodia irritans</i> R. Br.	+	-	+	-	-	-	+	+	+
<i>Velleia connata</i> F. Muell.	-	-	-	-	-	-	-	+	-
<i>Vittadinia dissecta</i> (Benth.) N. Burb.	-	-	+	-	-	-	-	+	-

TABLE 3 cont. Full species list (nomenclature following Jessop & Toelken 1986) showing occurrence in the seven major vegetation types. Occurrence in sites that could not be assigned to a major vegetation type are grouped in the final column. Introduced species are indicated with an asterisk.

Species	Vegetation Type								Other
	I	II	III	IV	V	VI	VII	Other	
<i>Westringia rigida</i> R. Br.	-	+	-	-	+	-	-	-	-
<i>Zygophyllum ammophilum</i> F. Muell.	+	-	-	-	-	-	-	-	-
<i>Zygophyllum apiculatum</i> F. Muell.	+	+	-	-	-	-	-	-	-
<i>Zygophyllum urantiacum/ovatum</i> (Lindley) F. Muell./Ewart & J. White	+	+	-	-	-	-	-	-	-
<i>Zygophyllum glaucum</i> F. Muell.	+	-	+	+	+	+	+	-	-

being very long-lived plants, may be indicating some historical influence, while the shorter-lived understorey species reflect current environmental conditions. Lange & Nicolson (1982) report mallees recording former extensions of a palaeosol, and Twidale & Campbell (1985) and Short *et al.* (1986) provide ample evidence of dynamic changes in the surface geology of north-western Eyre Peninsula during the Holocene.

A further issue is the occurrence of uncommon vegetation associations in the area. One example is the *Callitris preissii* association represented by a single site on the dendrogram; another, towards the northern end of the Mudamuckla transect and

removed from analysis due to disturbance, was unique for the presence of *Casuarina cristata*. A regular sampling strategy inevitably leads to the omission of rare vegetation types, so there are undoubtedly other uncommon associations in the area.

Acknowledgments

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TRANSACTIONS OF THE
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TIMING, EXTENT AND CHARACTER OF LATE, CAINOZOIC FAULTING ON THE EASTERN MARGIN OF THE MT LOFTY RANGES, SOUTH AUSTRALIA.

BY R. P. BOURMAN & J. M. LINDSAY†*

Summary

Stream erosion on the eastern flank of the Mt Lofty Ranges has exposed a reverse fault near Cambrai on the Milendella escarpment, indicating a compressive component to the uplift of the ranges. Cambrian rocks have been thrust over Pleistocene fanglomerates and Miocene limestone has been dragged up along the fault zone to an elevation of 160 m asl. This fault may indicate the reactivation of a compressive Palaeozoic fault during the Cainozoic. Diagnostic foraminifera have been identified in samples of the limestone, which is of the Early Miocene Mannum Formation (about 20 Ma), adding support to the unpublished view that the position of the limestone on the escarpment is due to tectonic uplift of 60-90 m since the Miocene.

KEY WORDS: Tertiary limestone, foraminifera, reverse faulting, Mt Lofty Ranges, South Australia.

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by R. P. BOURMAN* & J. M. LINDSAY†

Summary

BOURMAN, R. P. & LINDSAY, J. M. (1989) Timing, extent and character of late Cainozoic faulting on the eastern margin of the Mt Lofty Ranges, South Australia. *Trans. R. Soc. S. Aust.* **113**(1), 63-67, 31 May, 1989.

Stream erosion on the eastern flank of the Mt Lofty Ranges has exposed a reverse fault near Cambrai on the Milendella escarpment, indicating a compressive component to the uplift of the ranges. Cumbrian rocks have been thrust over Pleistocene fanglomerates and Miocene limestone has been dragged up along the fault zone to an elevation of 160 m asl. This fault may indicate the reactivation of a compressive Palaeozoic fault during the Cainozoic. Diagnostic foraminifera have been identified in samples of the limestone, which is of the Early Miocene Mannum Formation (about 20 Ma), adding support to the unpublished view that the position of the limestone on the escarpment is due to tectonic uplift of 60-90 m since the Miocene.

KEY WORDS Tertiary limestone, foraminifera, reverse faulting, Mt Lofty Ranges, South Australia.

Introduction

The fault origin of the Mt Lofty Ranges has long been discussed (Benson 1911; Fenner 1930; Sprigg 1945) and the majority of these workers considered that the faults were normal types. Glaessner (1953) presented a model for the tectonic evolution of the Mt Lofty Ranges, which involved basement complex flexuring, that resulted in reverse faulting on the margins of the ranges and normal faulting within them. Campana (1955) preferred to explain the origin of the Mt Lofty Ranges by compressional doming, which led to minor fault disruption on their margins. Gibson (1963)¹ noted that the Clarendon-Ochre Cove Fault displays a reverse habit where intersected by tunnelling operations during the construction of the Clarendon-Happy Valley pipeline. Recently Wellman & Greenhalgh (1988) favoured the view that compressive forces have been important in the formation of the Mt Lofty Ranges. A re-evaluation of exposed fault contacts is required to resolve the nature of the faulting responsible for the uplift of the Mt Lofty Ranges.

The Milendella Fault

There is clear evidence of reverse faulting on the eastern escarpment of the Mt Lofty Ranges as first reported by Mills (1965)², and it may indicate the

re-activation of Palaeozoic thrust faults. Stream exposures of the Milendella Fault occur west of Cambrai on the escarpment (Angaston MR 390/630) at 160 m asl (Fig. 1). The fault here is of reverse type with brecciated Cambrian schists of the Kanmantoo Group of metasedimentary rocks thrust over Pleistocene fanglomerates. Two pods of Tertiary limestone have been dragged up at a high angle in the fault zone, which dips to the west at 45° (Fig. 2). The Pleistocene fanglomerates affected by the faulting are similar to Pleistocene fanglomerates tilted into a vertical position by movement along the Willunga Fault at Sellicks Beach (May & Bourman 1984). The sediments at Sellicks Beach were related to the Ochre Cove Formation, which May & Bourman (1984) regarded as of Middle Pleistocene age. If the two deposits are correlative then faulting on the Milendella Scarp probably occurred until the late Middle Pleistocene or the early Late Pleistocene. No unequivocal evidence of dislocation of Late Pleistocene sediments in the area was noted.

It is suggested that during faulting, the Pleistocene fanglomerates were folded, and brecciated basement rocks broke from the hanging wall to tumble on top of the fanglomerates. Calcrete mantles the convoluted fanglomerates, dying out at the fault zone, so that the calcrete may have derived from solution and reprecipitation of the Tertiary limestones dragged to the surface along the fault zone and draped over the top of the fanglomerates. Calcareous pisoliths in this calcrete are typically laminated around cores of locally derived bedrock. This supports the interpretation of *in situ* pisolith formation from the redistribution of Tertiary limestone. Alternatively, if the calcrete has stratigraphic significance (e.g. the upper Middle Pleistocene Bakara calcrete of Firman 1967) then

¹ Gibson, A. A. (1963) Final geological report on the Happy Valley Tunnels Project. S. Aust. Dept. of Mines report 57/92 (unpubl.)

² Mills, K. J. (1965) "The structural petrology of the Milendella area of South Australia". Ph.D. Thesis, University of Adelaide (unpubl.)

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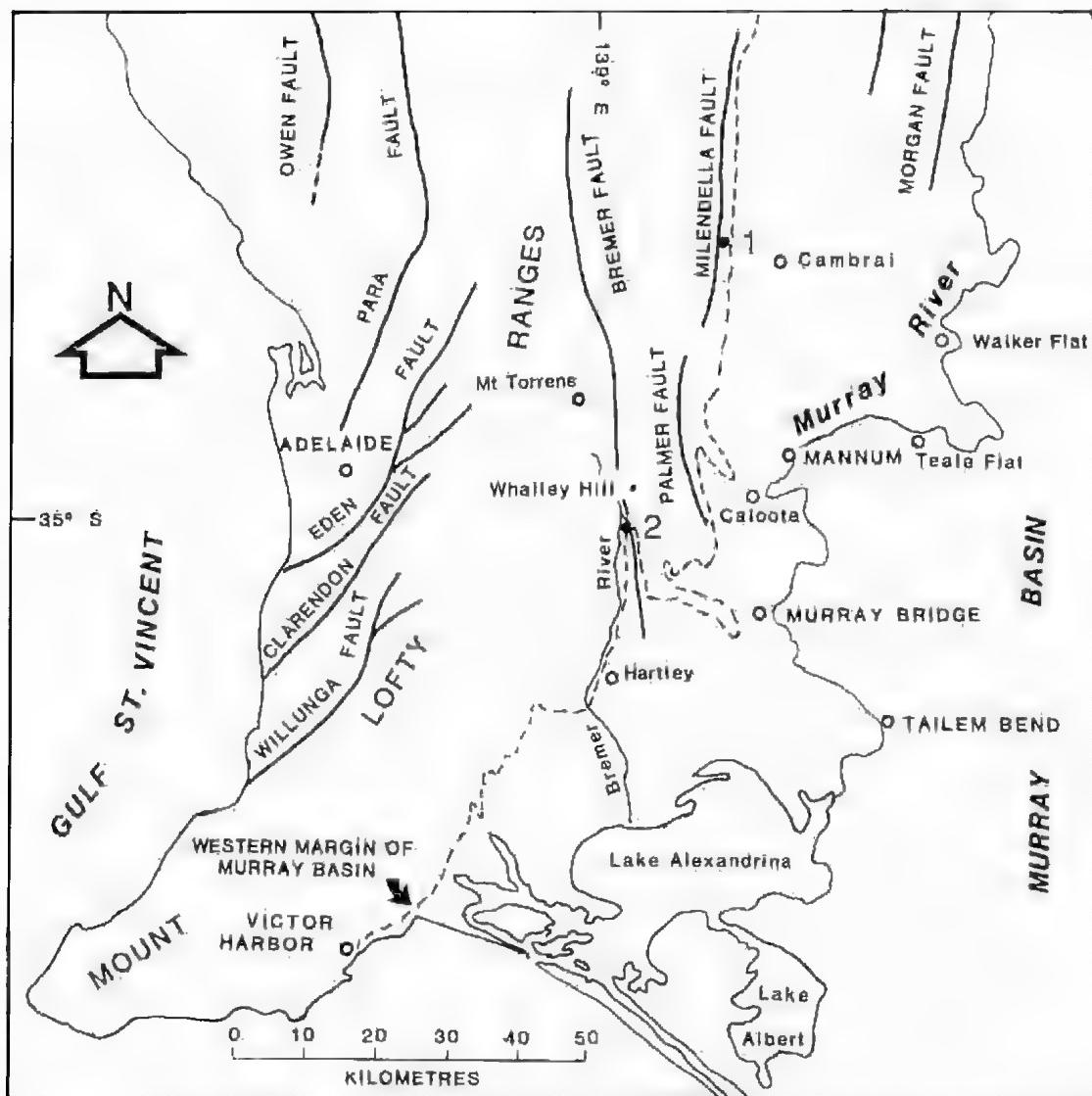


Fig. 1. Location map showing major fault zones, ¹ site of fault exposure near Cambrai and ² *Lepidocyrtina*-bearing limestone in the Bremer valley.

the relationships may indicate fault disruption of the calcrete in the Late Pleistocene. It is not possible to determine the amount of offset accomplished during this postulated Pleistocene phase of faulting without detailed drilling. However, Mills (1965)² shows a thickness of some 30 m of Pleistocene sediments in section at the scarp (Fig. 3), and as the limestone must have been dragged up from below this level, this suggests an offset of less than 30 m. Dislocation of Early Pleistocene marine sediments across the Willunga Fault was reported by May & Bourman (1984) illustrating similar post-Early Pleistocene faulting of about 40 m on the opposite side of the ranges. It is interesting to note

that although there is clear evidence of geologically recent faulting on the eastern margin of the Mt Lofty Ranges, there is no pronounced fault scarp associated with it, which may suggest that the scarp formed largely in brecciated rock and rapidly degraded.

Mills (1965)² suggested that displacement on the Milendella Fault since "pre-Tertiary peneplanation" was approximately 335–366 m, and he attributed 250 m of this to the Early Tertiary to Miocene, and 60–90 m to post-Miocene faulting. He noted Miocene sediments (?Morganian Limestone) at elevations up to 160 m on the scarp, correlated them with Miocene strata under the Murray Surface and

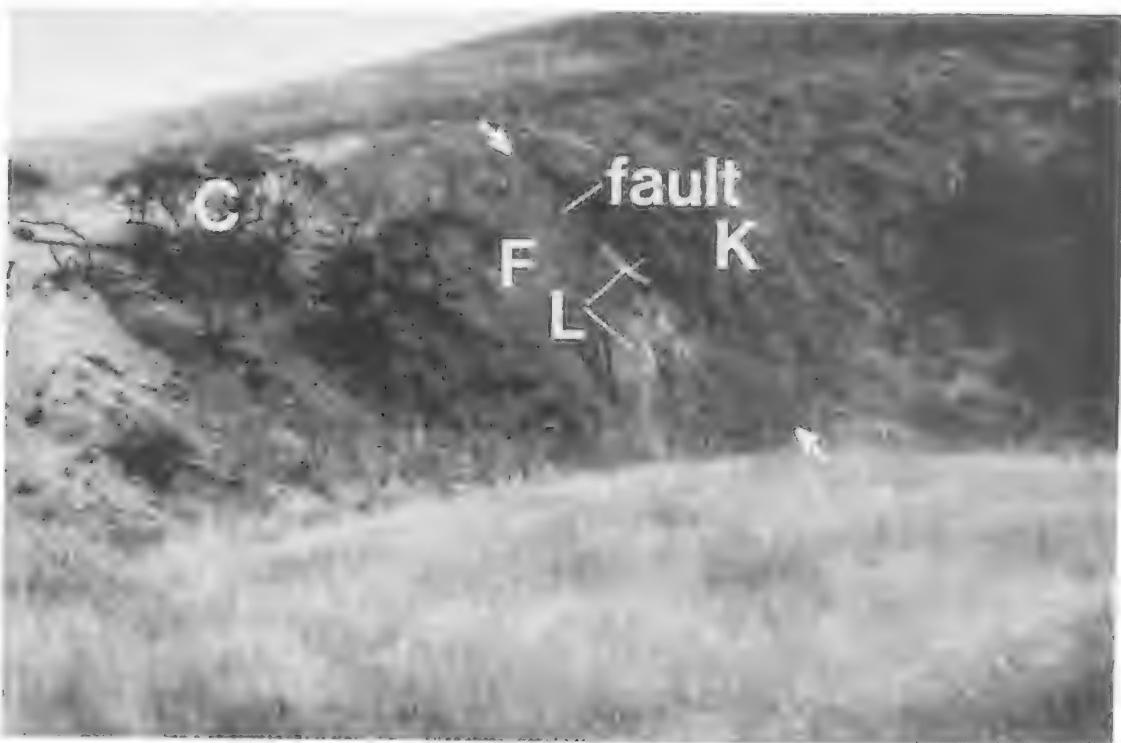


Fig. 2. Fault exposure near Cambrai. View south along the eastern escarpment of the Mt Lofty Ranges. Cambrian schists (K) of the Kanmantoo Group of metasedimentary rocks have been thrust over (?) Middle Pleistocene fanglomerates (F). Light coloured calcrete (C) mantles the fanglomerates and two pods of Miocene limestone (L) occur in the fault zone (arrowed), which dips to the west at approximately 45°.

attributed the difference in elevation to tectonic dislocation. Twidale & Bourne (1975) did not deny recent fault activity but preferred to interpret the perched limestone as essentially due to Tertiary eustatic influences, with the limestone under the Murray Basin being the older, lower Mannum Formation and that on the scarp as the younger and higher Morgan Limestone. Thus they discounted the view that there had been 60–90 m of dislocation on the Milendella Fault since the Miocene and argued for an erosional origin for the lower part of the scarp. The resolution of this conflict may be achieved only by an accurate age determination of the Miocene limestones on the Milendella scarp to compare with those from the Murray Basin. Palaeontological work reported here demonstrates that the limestone on the scarp, at least in this locality, is from the lower part of the Mannum Formation.

Age and facies of the Tertiary limestone in the fault zone

Four samples have been examined from the two pods of Tertiary limestone dragged up in the fault zone.

Portions were crushed gently in a pestle and mortar to disaggregate partially, boiled in a dilute solution of sodium bicarbonate with a drop of detergent, washed free of mud through a very fine sieve, dried, and picked for foraminifera under a binocular microscope. Slides with the foraminiferal microfaunas are stored in the Biostratigraphy Branch collections of the S. Aust. Department of Mines and Energy.

Lithology

All four samples comprise quartzose fossiliferous sandy limestone (biogenic calcarenite). The rocks are cream to brown, hard to friable, somewhat recrystallised and, in part, leached. Quartz and minor lithic sand content is considerable and poorly sorted, ranging from very fine grained to very coarse grained. Quartz and lithic grains up to 10 mm are present. There are occasional pale green glauconite infillings, somewhat oxidised.

Barnacle plates are frequent and notable; echinoid, molluscan and bryozoal fragments are frequent to common; foraminifera are common but mostly recrystallised; ostracods, *Ditrupa* tubes, fish and decapod fragments, and algal oncolites are rare.

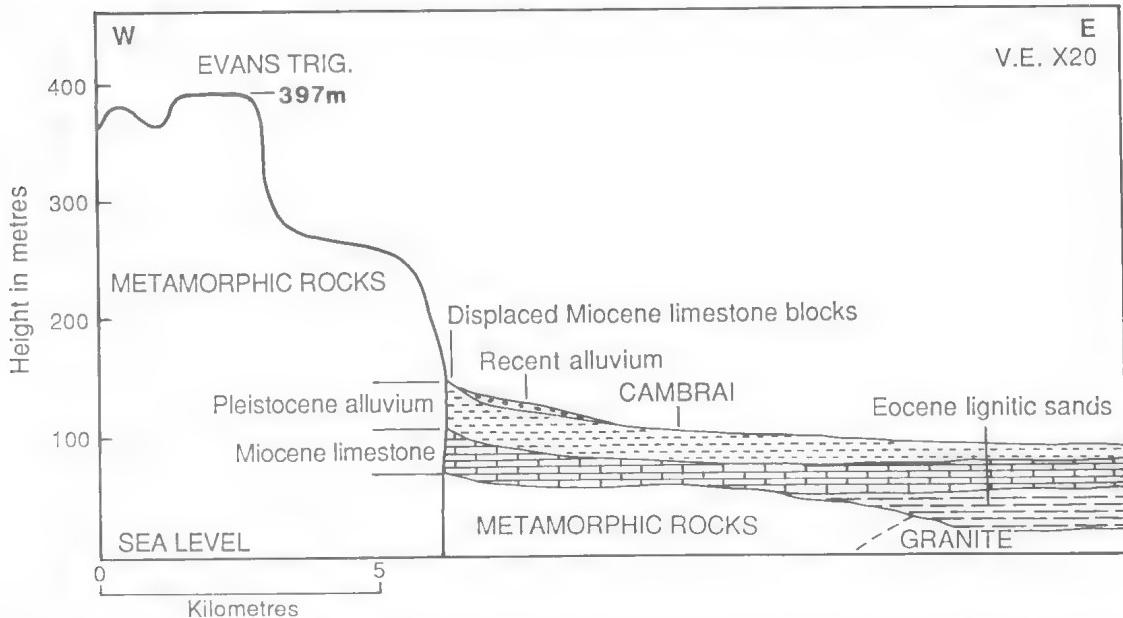


Fig. 3. Cross section through the eastern margin of the Mt Lofty Ranges to the Murray Basin near Cambrai (after Mills 1965²).

Discussion of foraminifera, age and correlation

The four samples have much in common and the microfaunas will be considered together (Table 1). Numerically, all the microfaunas are dominated by *Elphidium chapmani* and *Notorotalia cf. miocenica*, but these are not the most biostratigraphically significant.

The overlap of the top of the range of *Sherbornina atkinsoni* and the bottom of the range of *Operculina victoriensis* in S. Aust. indicates an early Longfordian, Early Miocene age (Wade 1964; Lindsay 1985). For the Murray Basin proper,

Ludbrook (1961) only overlapped these ranges in lower Mannum Formation, and this has been borne out by subsequent experience. Other foraminifera present in the four samples are generally consistent with Longfordian Stage and Early Miocene age. *Notorotalia miocenica* has been scarcely recorded previously from S. Aust., so the slightly earlier age here of a related form, compared with the range in Victoria (Carter 1964) is not regarded as incongruous. The solitary and small planktonic specimen identified as *Globigerina* sp. is non-diagnostic.

TABLE 1. Foraminifera: Table of occurrences of selected species.

Foraminifera	F23/83	F24/83	Samples F2/88	F3/88
<i>Discorbis</i> sp. from group D. <i>balcombensis</i>				
Chapman, Parr & Collins -D. <i>cycloclypeus</i>				
Howchin & Parr	R	R	F	F
<i>Ammonia</i> sp.	-	V	-	R
<i>Pararotalia verriculata</i> (Howchin & Parr)	V	V	-	V
<i>Sherbornina atkinsoni</i> Chapman	-	-	-	V
<i>Elphidium chapmani</i> Cushman	C	C	A	A
<i>E. crassatum</i> Cushman	F	R	C	F
<i>E. parri</i> Cushman	-	-	-	V
<i>Notorotalia cf. miocenica</i> (Cushman)	F	F	C	A
<i>Operculina victoriensis</i> (Chapman & Parr)	V	R	V	R?
<i>Globigerina</i> sp.	-	-	-	V
<i>Amphistegina</i> sp.	-	-	-	R
<i>Cibicides vortex</i> Dorreen	-	-	V	-
<i>Planolinderina plana</i> (Heron-Allen & Earland)	-	-	V	-

(Abundances: V = very rare; only one or two specimens recovered in thorough picking. R = rare; 3-5. F = frequent; 6-10. C = common; 11-25. A = abundant; more than 25).

The lithology of the samples is consistent with, but not unique to, Mannum Formation as described by Ludbrook (1961) and observed subsequently. This Early Miocene Mannum Formation in the fault zone is distinctly older than the elevated, *Lepidocyrtina*-bearing, Morgan limestone reported from the Bremer valley east of Kanmantoo (Lindsay 1986²); about 20 Ma compared with 16 Ma (Lindsay 1985).

Environment of deposition

The variety and nature of the fauna indicate marine conditions. Three lines of evidence suggest a shallow-marine littoral-neritic environment: the notable frequency of barnacle remains, the restricted *Elphidium*-rich foraminiferal facies almost lacking planktonic forms, and the quartzose and lithic clastic component of the limestone, with gravel-sized grains. This corroborates the sedimentological evidence of Mills (1965)², who proposed a near-shore environment for the deposition of the limestone.

Conclusion

The evidence presented here demonstrates that most of the elevational difference between the

Mannum Formation limestones on the escarpment, near Cambrai, and under the Murray Basin can be attributed to tectonic dislocation in the past 20 Ma as originally suggested by Mills (1965)². Furthermore, it has also been demonstrated that there has been at least 100 m (and probably much more) of tectonic offset of the early Middle Miocene *Lepidocyrtina*-bearing Morgan Limestone that occurs in the Bremer Valley (Lindsay 1986)² in the past 16 Ma. Consequently, evidence of considerable tectonic dislocation of Tertiary limestones on the eastern side of the Mt Lofty Ranges, separated by 50 km, together with faulted Pleistocene sediments provides strong support for pronounced tectonism since the Middle Miocene. Without denying the evidence for eustatic influences in the Tertiary (e.g. Vail & Hardenbol 1979) it is clear that post Middle Miocene faulting is far more significant in the evolution of the east Mt Lofty Ranges than suggested by Twidale & Bourne (1975). Furthermore, the clear exposure of a reverse fault on the eastern margin of the Mt Lofty Ranges supports the notion of a compressive component to the forces involved in the Tertiary uplift of the eastern Ranges.

Acknowledgments

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INTERTIDAL COMMUNITIES OF NORTHERN SPENCER GULF, SOUTH AUSTRALIA

*BY R. C. AINSLIE, D. A. JOHNSTON & E. W. OFFLER**

Summary

The fauna of the intertidal mudflats of northern Spencer Gulf was monitored between 1982 and 1986. Two main habitats were identified, the mid intertidal zone, and the seagrass fringing low intertidal zone. These habitats supported quantitatively differing faunas.

There was no evidence of the species impoverishment reported elsewhere for the epizoic fauna of this region. Comparison of the characteristics of the fauna with that of another negative estuary, the Port River in Gulf St Vincent, has provided the basis of a monitoring programme to assess potential environmental stress imposed by power station development in northern Spencer Gulf.

KEY WORDS: Intertidal habitats, benthic fauna, seagrass, Spencer Gulf.

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Introduction

Northern Spencer Gulf can be defined as that portion of Spencer Gulf, South Australia, north of the line from Ward Spit to Lowly Point, i.e. north of 33°S (Stefanson 1977). It is a unique, narrow body of water, projecting inland some 200km from the Southern Ocean coast (Fig. 1).

The waters of northern Spencer Gulf are characterised by high summer salinities, up to 48 (Nunes & Lennon 1986) and high summer temperatures with wide seasonal fluctuations, 11–25°C (Johnson 1981¹). Due to high evaporation, and low fresh water inflow to the northern Gulf, there is a longitudinal salinity gradient of about four in 20km. The region has been described as a negative estuary.

A limited number of studies has been carried out on the marine communities of the "middle Gulf" (SEA 1981²; Ward & Young 1982, 83) and concur-

rently with this study, Kinhill (1987)³ have examined intertidal communities at Ward Spit and Lowly Point. Shepherd (1983) provides the only published description of benthic communities of the narrow reaches of the northern Gulf. Shepherd found a marked reduction in species number in the epizoic communities on *Pinna bicolor* in northern Spencer Gulf compared to that of the same habitat in Gulf St Vincent, raising the possibility of a general species impoverishment in the hyper-saline waters of northern Spencer Gulf. He emphasised the need for further detailed study of other "component parts" of the biological system to determine its capacity to accept additional stresses of industrial wastes and discharges.

Since the mid 1950's Playford Power Station has been operating on the eastern shore of the northern Gulf, discharging warmed cooling water to the Gulf. The discharge from Playford Power Station, operating at its maximum nominal capacity of 330MW, resulted in surface water temperatures about 6°C above ambient near the power station, with only occasional incursions of warmed water (about 3°C above ambient) to nearby intertidal zones (ETSA 1977⁴). In 1977 and 1985 the Electricity Trust of South Australia issued Environmental Impact Statements for three further power station units, with a total generating capacity of 750MW, to be built in this area. This development forms the Northern Power Station. Thermal discharges were predicted to more than double (ETSA 1977⁴, 1985⁵).

The effects of warm water discharge from power stations on benthic fauna have been the subject of a number of reviews (Coutant & Talmage 1975; Talmage & Coutant 1980; Craven *et al* 1983; Langford 1983). Effects vary from site to site as a

¹ Johnson, J.E. (1981) Hydrological Data for Upper Spencer Gulf 1975–1978. Fisheries Res. Paper No. 3, 1–30, (Dept. Fisheries, Adelaide), unpubl.

² Social and Ecological Assessment (1981) Draft Environmental Impact Statement for port and terminal facilities at Stony Point, South Australia. Prepared for SANTOS, unpubl.

³ Kinhill (1987) Upper Spencer Gulf Intertidal Survey. Final Report, May 1987, unpubl.

⁴ Electricity Trust of South Australia (1977) Northern Power Station Environmental Impact Statement. July 1977, unpubl.

⁵ Electricity Trust of South Australia (1985) Northern Power Station Environmental Impact Statement. August 1985. Prepared by Kinhill Stearns, unpubl.

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function of the climatic, hydrological and biological features (Crema & Pagliai 1980). Greatest effects are observed near the outfalls, at the hottest times of the year (Langford 1983) and include changes in the biological characteristics of the benthic communities within the zone of influence of the warm water plume (Robinson *et al.* 1983; Robinson 1985; Thomas *et al.* 1986). In particular, Bamber & Spencer (1984) and Thomas *et al.* (1986) have described the decline in populations of particular bivalve mollusc species and the establishment of dense populations of opportunistic worm species as characteristic of thermal disturbance in soft substrates.

The present study began in 1982, three years prior to the commencement of operation of the new power station. Intermittent operation of the first 250MW unit commenced in the summer of 1985, with 500MW operating by summer 1986. The aim of the study was to investigate spatial and temporal patterns of the benthic communities in the negative estuary of northern Spencer Gulf. It was anticipated that detailed descriptions of these communities would identify whether or not there were any biological impacts from the existing power station development (and early operation of the new development), and establish baseline data for long term assessment of the effects of increased thermal discharge. This study concentrated on the intertidal and shallow sublittoral fringe, as the only other published South Australian study on the impacts of thermal discharge on the marine environment had described well defined patterns of change in the communities of this zone (Thomas *et al.* 1986).

The influence on communities of sediment type, degree of emersion, and presence of seagrass are investigated in this study.

Station locations, elevations, and sediments.

Near Port Augusta the narrow channel basin of northern Spencer Gulf is bordered by shallow sublittoral seagrass meadows and extensive intertidal mudflats backed by stands of the grey mangrove, *Avicennia marina* var. *resinifera* (Fig. 1).

Seven transects were established along the eastern shore of the gulf, both adjacent to and remote from, existing and proposed power station developments (Fig. 1). Three stations were established at different intertidal zones on each transect. Each station had an area of about 25m². On each transect, station 1 was located 30m seaward from the mangrove fringe, station 3 was located at the seagrass verge, (emergent at extreme low tide) and station 2 was located midway between 1 and 3. The locations and elevations of each station were confirmed relative to an established Port Augusta Power Station datum, using an EDM theodolite.

Sediment samples were collected from each station on all transects and analysed for grain size according to the Wentworth scale (Folk 1968) with minor modifications (Thomas *et al.* 1986). Graphic means, Mz, (Folk 1968) were determined for the samples. The Bray-Curtis classification technique was used to determine homogeneity groups based on the percentage distribution of particular sediment size classes in each sample (Miedeke & Stephenson 1977; Thomas *et al.* 1986).

Water and air temperature.

For the study period 1982–1986, a continuous record of Gulf water temperature was made at the cooling water intakes of Playford Power Station. A continuous three hourly record of ambient air temperature was made at the SA Weather Bureau's Port Augusta weather station No. 019066.

Fauna

Each station was sampled using a hand operated coret collecting a sediment sample of 1600 cm³, surface area 80 cm², to a depth of 20 cm. The samples were taken during daylight hours.

The pattern of species accumulation with repeated random coring within a station area was determined. By subsample 20, about 90% of the species recorded in 40 subsamples had been found, and those species which occurred after subsample 20 comprised an extremely small number of the total number of individuals sampled. The decision was made to proceed using 20 subsamples per station, exceeding the species-area requirements proposed by Cain & Castro (1959) and meeting the stringent proposals of Weinberg (1978). Each station was sampled twice yearly (winter and summer) from June 1982 to June 1986. Samples were treated as described in Thomas *et al.* (1986). Faunal relationships (between stations, transects, tidal zones, and sampling times) were interpreted using Bray-Curtis classification after root-root transformation of the data, and dendograms were constructed with group average sorting (Swartz 1978; Field *et al.* 1982).

Species constancy, abundance rank scores, and average rank scores were assigned as in Haulstone (1976) for 160 species totalling 34,312 individuals.

Species associations were determined using Bray-Curtis classification analysis on non-transformed data, considering the 40 top ranked species for the period 1982–1986.

Results

Station elevations and sediments

Tidal fluctuations relative to station zones result in different periods of emergence for stations 1, 2 and 3 on all transects. Considering February 1984,

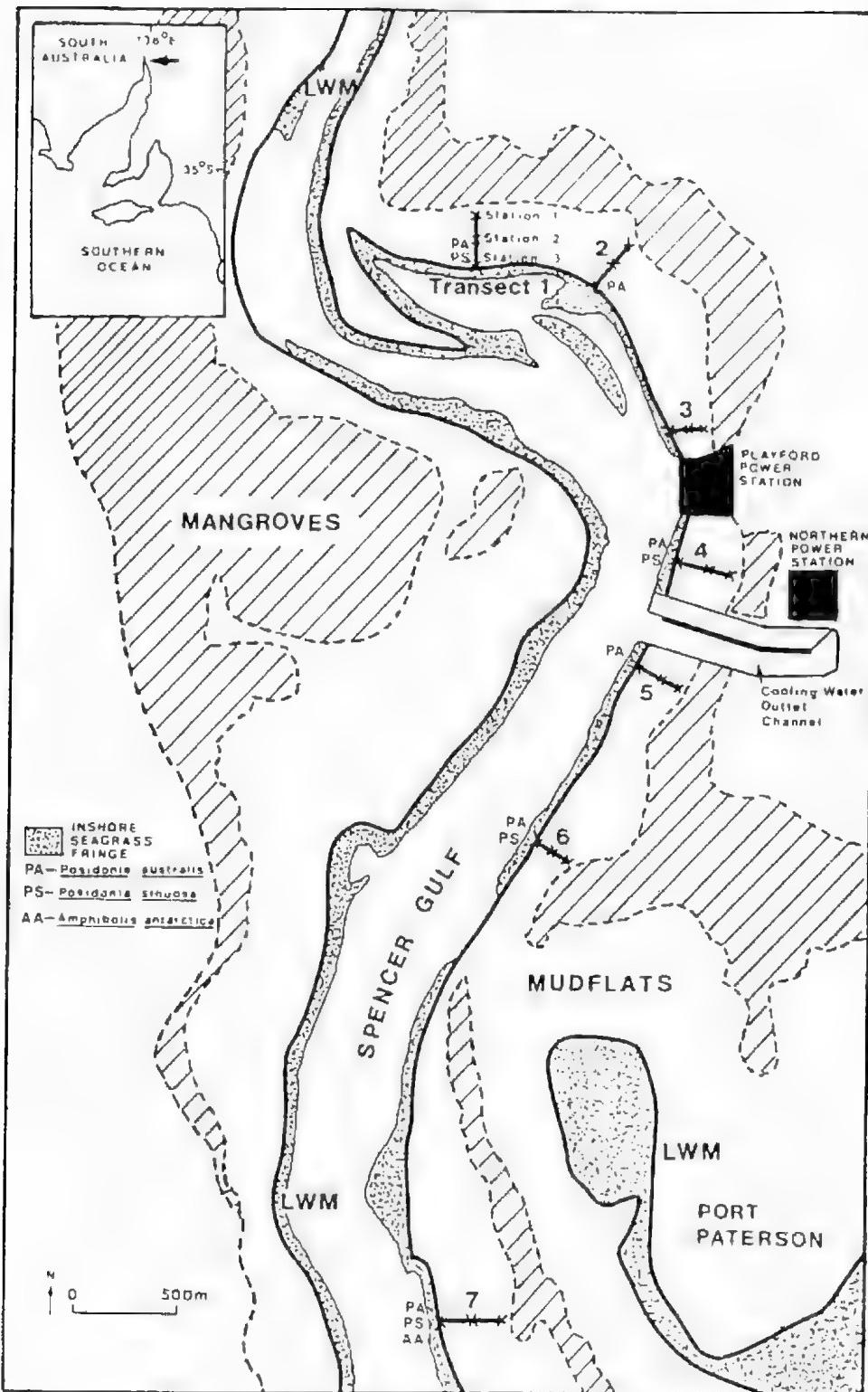


Fig. 1. Sampling station locations. Northern Spencer Gulf, South Australia. Inshore fringing seagrass species also denoted.

the station 1 zone is emergent for over 200 hours/month, station 2 for about 80 hours/month, and station 3 for about 5 hours/month, or less than 1% of the time. In winter even shorter periods of emergence occur at the low intertidal zone. Local meteorological conditions, such as wind velocity, also affect the degree of exposure on low spring tides. Thus stations 1 and 2 are clearly mid intertidal stations while station 3 is in the low intertidal zone.

The mid intertidal stations are devoid of seagrass cover. The seagrass species at stations 3 include both *Posidonia australis* and *Posidonia sinuosa*, without clear zonation in the shallow water. Some *Amphibolus antarcticus* is present at transect 7.

The hierarchical classification of sediments from all stations gives two major groups of stations, groups (a) and (b) (Fig. 2). The sediments of stations forming group (a) have Mz values which generally range from medium sand (1.5ϕ) to coarse sand (0.25ϕ). The exceptions are station 1.1 which is classified as fine sand ($Mz = 2.5\phi$), and the subgroup formed by sediments of stations 6.1 and 6.2. These last two stations have Mz values between 0 and -0.25ϕ (i.e. at the lower end of the very coarse - sand scale).

The second major group of sediments (b) have Mz values ranging from very coarse sand (-2.5ϕ) through to granules (-1.7ϕ), with stations 7.1 and 7.2 having the coarsest sediments recorded in the survey. Although sediments of station 7.3 have an Mz value of 1.25ϕ (medium sand), this station forms its own subgroup on the dendrogram because of the restricted distribution in grain size around the median, unlike all other samples which had more or less even ranges of grain sizes.

Air and water temperatures

Air and water temperatures 1982, 1984 and 1985 show that seasonal water temperatures follow air temperatures. Ambient average monthly water temperatures range from 11–12.5°C in winter to 24–25°C in summer (Fig. 3).

There is no indication of change in the overall ambient temperature from 1982–1985, as a result of intermittent cooling water discharge from the existing power station development.

Fauna

A total of 160 species were recorded; polychaetes were the most numerous with 52 species, including several new records for S. Aust. (Table 1). Molluscs with 50 species and crustaceans, 40 species, were next in abundance, with 18 species from various other taxa (Table 1).

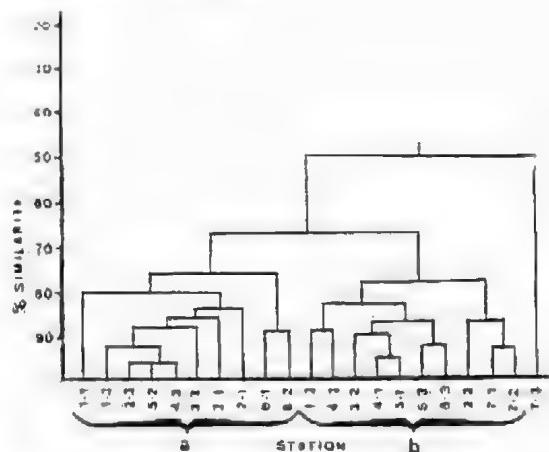


Fig. 2. Dendrogram of northern Spencer Gulf stations by sediment grades.

Fig. 4 presents the station faunal homogeneity dendograms for the first two seasonal surveys (winter 1982, summer 1983), and for the last two surveys (summer and winter 1986). In all cases, at about the 25–30% level the homogeneity dendograms consistently show two major collection clusters with high intra-group homogeneity (Fig. 4 (1–4), Groups A and B). Generally the faunas of stations 1 and 2 on all transects comprise Group A on each dendrogram, and station 3 faunas form Group B. In two of the dendograms presented (winter 1982 and summer 1986) there are exceptions to this generalisation, but there is no seasonal or spatial pattern to the exceptions, and the major trend persists. There is no evidence of consistent subgrouping within the major observed associations (Group A and Group B, Fig. 4). This tendency for faunas of mid intertidal stations 1 and 2 to group more closely together than to those of station 3 has been consistent throughout the four year study period and is also reflected in the tidal zone analysis (Fig. 5) for each survey 1982–1986.

The species homogeneity dendrogram determined using the 40 most common species is presented in Fig. 6. Accepting the arbitrary cut-off level of 25% similarity, this dendrogram shows two major groups of species (A1 and B1, Fig. 6). Although all but two of the forty most common species occur over all stations, those which form Group A1 always contribute a greater proportion of the total number of individuals in the samples of stations 1 and 2 and those of Group B1 are always more abundant in the station 3 faunas.

Together these analyses (Figs. 4, 5 & 6) indicate that the two habitats represented by the mid intertidal region (stations 1 and 2) and the low interti-

TABLE 1. Species recorded throughout the study. New records for South Australia are indicated by an asterisk.

	Exclusively mid intertidal	Exclusively low intertidal
POLYCHAETES		
<i>Olganereis edmondsi</i> (Hartman)		
<i>Neanthes vaalii</i> Kinberg		
<i>Neanthes cricognatha</i> (Ehlers)		
<i>Ceratonereis transversa</i> Hutchings & Turvey		
<i>Ceratonereis mirabilis</i> Kinberg		+
<i>Perinereis nuntia</i> (Grube)		
<i>Perinereis amblyodonta</i> (Schmarda)	+	
<i>Perinereis</i> sp		
<i>Nereis triangularis</i> Hutchings & Turvey		
<i>Nereis</i> sp		+
<i>Nematoneureis unicornis</i> (Grube)*		+
<i>Marpissa</i> sp*		+
Arabellidae 1*		+
Arabellidae 2*		+
<i>Lysidice</i> sp		
<i>Eunice</i> sp		+
<i>Schistomerings</i> sp		
<i>Lumbrinereis</i> sp		
<i>Nephtys australiensis</i> Fauchald		
<i>Glycera americana</i> Leidy		
<i>Phylo</i> sp*		+
<i>Scoloplos cylindriger</i> Ehlers		
<i>Leitoscoloplos normalis</i> Day*		
<i>Leitoscoloplos</i> sp		
<i>Naineris grubei australis</i> Hartman		
Phyllodocidae 1*		+
Phyllodocidae 2*		+
Phyllodocidae 3*		+
<i>Cirriformia filigera</i> (Grube)	+	
Cirratulidae sp		
<i>Boccardia chilensis</i> Blake & Kudenov		
<i>Harmothoe</i> sp 1^		+
<i>Harmothoe</i> sp 2^		+
<i>Harmothoe</i> sp 3^		+
<i>Lysilla aphaeles</i> Hutchings*		
<i>Liomia medusa</i> (Savigny)*		
<i>Eupolymlnia nebulosa</i> (Montague)		
<i>Streblosoma</i> sp*		
Terebellinae 1		
Terebellinae 2		+
Terebellinae 3		+
Terebellinae 4		+
Polycirrinae*		+
A - species separated on basis of anterior elytrae.		
<i>Barantolla leptae</i> Hutchings		
<i>Notomastus</i> sp		+
Paraonidae		
<i>Pherusa</i> sp		
<i>Armandia</i> sp		
<i>Galeolaria caespitosa</i> (Savigny)		
<i>Scalibregma</i> sp*		+
Maldanidae*		+
<i>Magelona</i> sp*		+
NEMERTEAN		
Nemertean spp	+	
SIPUNCULID		
<i>Golfingia margaritacea adelaideensis</i> Edmonds		

	Exclusively mid intertidal	Exclusively low intertidal
BIVALVES		
<i>Tellina deltoidalis</i> Lamarck		
<i>Laternula recta</i> (Reeve)		
<i>Katelysia peronii</i> Lamarck		
<i>Katelysia scalarina</i> (Lamarck)		
<i>Brachidontes erosus</i> (Lamarck)		
<i>Xenostrobus inconsans</i> (Lamarck)		
<i>Ostrea angasi</i> Sowerby		
<i>Pinna bicolor</i> Gmelin	+	
<i>Malleus meridianus</i> Cotton	+	
<i>Anomia trigonopsis</i> Hutton		
<i>Circe scripta</i> Cotton		
<i>Electroma georgiana</i> (Quoy & Gaimard)		+
<i>Trichomya hirsuta</i> Lamarck		
<i>Chlamys bisrons</i> Lamarck		+
<i>Musculus paulucciae</i> Crosse		+
<i>Corbula flindersi</i> Cotton		+
<i>Lucilinidae</i>		+
GASTROPODS		
<i>Salinator fragilis</i> (Lamarck)		
<i>Nassarius burchardi</i> (Philippa)		
<i>Nassarius pauperatus</i> (Lamarck)		
<i>Monodonta constricta</i> Lamarck		
<i>Bembicium melanostomum</i> (Gmelin)		
<i>Batillaria estuarina</i> (Tate)	+	
<i>Batillaria diemenensis</i> (Quoy & Gaimard)		
<i>Bedeva paivae</i> (Crosse)		
<i>Cominella erburnea</i> (Reeve)		+
<i>Cominella</i> sp		
<i>Austroliotia densilineata</i> (Tate)		
<i>Diala lauta</i> A. Adams	+	
<i>Quibulla tenuissima</i> Sowerby		
<i>Lepsiella vinoso</i> Lamarck		
<i>Conus anemone</i> Lamarck		+
<i>Cantharidus irisodontes</i> (Quoy & Gaimard)		
<i>Clanculus plebejus</i> (Philippi)		
<i>Clanculus weedingi</i> (Cotton)		+
<i>Phasianella australis</i> (Gmelin)	+	
<i>Hydrobia</i> sp		
<i>Microcolus</i> sp	+	
<i>Sophisma lepas nigrita</i> (Sowerby)		+
<i>Pterynotus triformis</i> (Reeve)		+
<i>Nudibranchiata</i>		
<i>Opisthobranchia</i>		
<i>Notomella</i> sp		+
<i>Elegidion occiduum</i> Cotton		
<i>Asteracmea</i> sp 1		
<i>Asteracmea</i> sp 2	†	
<i>Stomatella auricula</i> (Lamarck)		
CHITONS		
<i>Ischnochiton variegatus</i> Adams & Angus		+
<i>Ischnochiton contractus</i> Reeve		+
<i>Heterozona</i> sp		
CEPHALOPODS		
<i>Haplochlaena maculosa</i> Quoy & Gaimard		

	Exclusively mid intertidal	Exclusively low intertidal
DECAPODS		
<i>Penaeus latisulcatus</i> (Kishinonye)		
<i>Processa gracilis</i> (Baker)	+	
<i>Leander serenus</i> (Heller)		
<i>Leander intermedius</i> (Stimpson)	+	
<i>Paguristes frontalis</i> (M. Edwards)	+	
<i>Paguristes brevirostris</i> (Baker)	+	
<i>Callianassa aequimana</i> (Baker)	+	
<i>Callianassa ceramica</i> (Fulton & Grant)	+	
<i>Crangon socialis</i> (Heller)		
<i>Pilumnus fissifrons</i> (Stimpson)		
<i>Philyra laevis</i> (Bell)		
<i>Cryptocnemus vincentianus</i> Hale		
<i>Polyonyx transversus</i> (Haswell)	+	
<i>Gomeza bicornis</i> (Gray)	+	
<i>Halicarcinus ovatus</i> (Stimpson)	+	
<i>Litocheira hispinosa</i> (Kinahan)	+	
<i>Portunus pelagicus</i> (Linnaeus)	+	
<i>Helograpus haswellianus</i> (Whitelegge)		
<i>Ceratoplaax punctata</i> (Baker)	+	
AMPHIPODS		
<i>Maera mastersii</i> (Haswell)		
<i>Birubius panamunus</i> Barnard & Drummond	+	
<i>Elasmopus bampo</i> Barnard		
<i>Allorchestes compressa</i> (Dana)		
<i>Ceradocus serratus</i> (Bate)	+	
<i>Cymadusa</i> sp		
Gammaridae 1		
Gammaridae 2	+	
Gammaridae 3	+	
ISOPODS		
<i>Cymodoce longicaudata</i> (Baker)		
<i>Zuzara venosa</i> (Stebbing)	+	
<i>Exosphaeroma</i> sp	+	
<i>Cirolana woodjonesi</i> (Hale)		
Cymothoidae		
Anthuridae 1	+	
Anthuridae 2	+	
TANAIDS		
<i>Apsuedes australis</i> (Haswell)		
<i>Paratanais ignotus</i> (Chilton)		
Tanaidac		
CIRRIPEDS		
<i>Balanus amphitrite</i> Darwin		
<i>Elminius modestus</i> Darwin		
CNIDARIANS		
<i>Anthothoe albocincta</i> (Stuckey)		
<i>Cricophorus nutrix</i> (Stuckey)	+	
PISCES		
<i>Nesogobius hinsbyi</i> (McCulloch & Ogilby)		
<i>Gymnapistes marmoratus</i> (Cuvier & Valenciennes)		
Plotosidae	+	

	Exclusively mid intertidal	Exclusively low intertidal
ECHINODERMS		
<i>Leptosynapta dolabrifera</i> (Stimpson)		
<i>Taeniogyrus roebucki</i> (Joshua)	+	
<i>Amblypneustes</i> sp		
<i>Trichodotus</i> sp	+	
Ophiuroidea 1		
Ophiuroidea 2		
Dendrochirotida		
Echinoidea		
ASCIDIANS		
<i>Ascidia</i> sp		+
DIPTERA		
Dolichopodidae	+	

dal fringe (stations 3) can be considered to have quantitatively differing faunas.

Fig. 7 compares mean number of species/m², and mean numbers of individuals/m² for these two habitats over the period 1982–1986. Significantly more species/m² are found in the low intertidal stations. Reference to the species list for all surveys reveals that of the 160 species collected, 86 (54%) occur over the whole tidal range. This 55% includes 37 of the 40 most common species. Fifty-nine species, or 38% of the total, occur exclusively in the low intertidal zone, and only 8% occur exclusively in the mid intertidal zone occupied by stations 1 and 2 (Table 1). In contrast to species abundance, the communities of mid intertidal stations 1 and 2 consistently have significantly higher mean numbers of individuals (Fig. 7) than those of the seagrass fringing stations 3. Nine of the 10 most common species are more abundant at stations 1 and 2 (Table 2, Fig. 6); conversely, of the 61 species exclusive to the station 3 community, only two appear in the "top 40" list (Table 2). Nevertheless the less common, but exclusively station 3 species, contribute to the consistent separation on the station and tidal zone faunal homogeneity dendograms (Figs. 4 and 5).

Fig. 8 shows the intersurvey time dendograms comparing whole survey collections for each of the two communities for the period 1982–1986.

Discussion

Community-habitat relationships of the mid intertidal and low intertidal zones.

In many studies sediment characteristics have been shown to be a significant factor in determining benthic community patterns (Gray 1974; Saenger *et al* 1982; Jones *et al* 1986). In intertidal

regions particularly, there is the potential for wave action to grade sediments, resulting in coarser particles on the upper shore line. Such a graded series of sediments is potentially reflected in the nature of the benthic communities (Gage 1974; Robinson 1985). On the low energy shore of northern Spencer Gulf there is no sediment gradation, with random groupings of station sediments irrespective of the zones in which the stations occur. There is a high overall similarity in the sediments, the two main groups discerned (medium to coarse sand, and coarse sand to granules) showing about 70% similarity on the homogeneity dendrogram (Fig. 2). In common with other studies of the South Australian Gulfs where a limited range of sediments is found (Kinhill 1987; Thomas *et al* 1986) there is no evidence that this factor influences benthic community distributions in the northern Spencer Gulf.

The mid intertidal zone is characterised by species which, although more common in this zone, occur over the whole tidal range (Table 1). The most abundant species is the mussel, *Brachidontes erosus*, which forms dense mats in this zone. Such mussel mats are characteristic of many low energy sand and mud flat substrata in S. Aust. (Womersley & Thomas 1976; Thomas *et al* 1986). Other bivalves, although less abundant than the mussels, are also characteristic of the mid intertidal zone. These include *Tellina deltoidalis*, a species belonging to a genus known to have a behavioural response to light direction which contributes to its zone maintenance (Newell 1979), *Katelysia scalarina*, and *Laternula recta*. These bivalves contribute to the abundance of many other species as they provide the substratum for the settlement of the barnacles *Elminius modestus* and *Balanus amphitrite*.

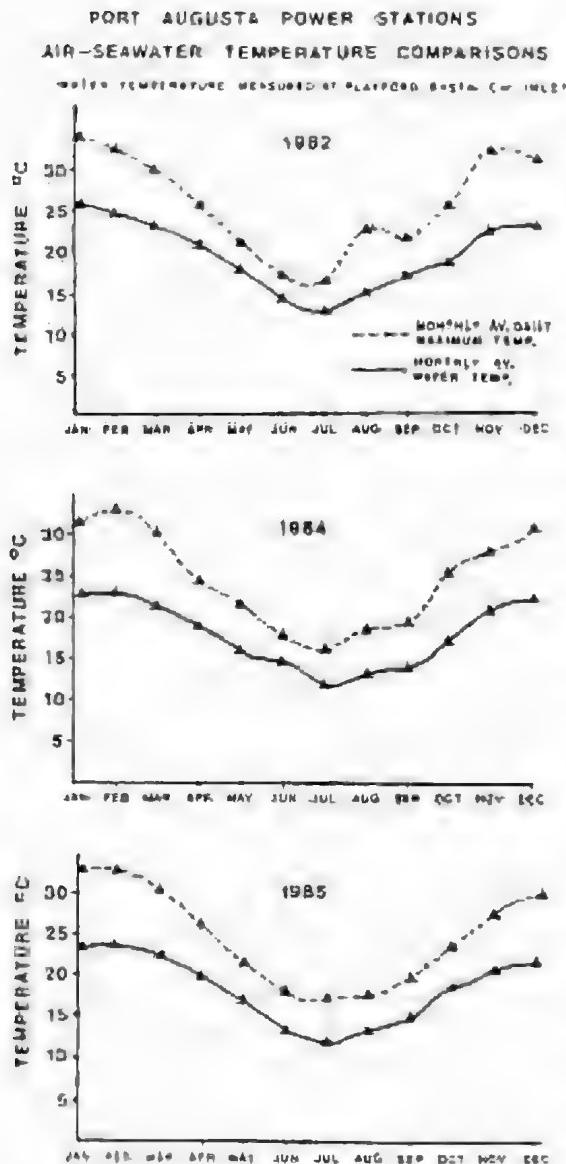


Fig. 3. Monthly averages of daily maximum air temperatures recorded at SA Weather Bureau Station No 019066, Playford Power Station, Pt Augusta (Fig 1). Monthly average ambient Gulf water temperature derived from continuous hourly records at the circulating water intakes, Playford Power Station.

trite, and the sea anemone *Anthothoe albocincta*. There also appears to be a close relationship between the large bivalve species and the omnivorous worm species *Nephtys australiensis*, *Neanthes vaalii*, *Oliganereis edmondsi*, and *Nereis triangularis*. The last species seems generally to be associated with mussel beds (Hutchings & Murray 1984). Several species of scavenging and carnivorous snails (*Nassarius pauperatus*, *Bedeva pa-*

vae, *Batillaria estuarina*, and *Batillaria diemenensis*) also occur in the community dominated by the mussel beds; as does the scavenging crab *Philyra laevis*, characteristic of the mid intertidal zone on low energy coastlines of S. Aust. (Womersley & Thomas 1976). The herbivorous top shell, *Monodonta constricta* is common among the dense mussel beds which provide a substrate for algal growth, particularly *Enteromorpha spp.*

In the extreme weather conditions of the northern Spencer Gulf it is clear that a number of ubiquitous intertidal species are restricted to the low intertidal zone. These include the polychaetes *Nematoneis unicornis*, *Ceratonereis transversa*, *Barantolla leptae*, *Cirriformia filigera* and *Leltoscoloplos normalis*, for which a range of habitats has been documented (Hutchings & Murray 1984) and the gastropods *Nassarius burchardi*, and *Austroliotia densilineata*, also found elsewhere over broad tidal ranges (Thomas et al 1986). Conversely, there are a number of species which are generally characteristic of the subtidal zone. These include such species as the hammer oyster *Malleus meridianus*, the scallop *Chlamys bifrons*; the blue swimmer crab *Portunus pelagicus*, and several other species primarily, or only, found in association with seagrass (*Electroma georgiana* (Ludbrook 1984), *Golfingia margaritacea adelaideensis* (Edmonds 1980) and *Amblypneustes* sp. (Shepherd & Spragg 1976)). The major environmental factor which appears to separate the habitats described in this study is the "degree of exposure". This is a function not only of the length of the periods of emersion (in a region of high summer air temperatures) but also the protection from environmental extremes provided by the presence of seagrass in the low intertidal zone.

Comparisons with other areas.

Are the intertidal communities of northern Spencer Gulf impoverished as evidence may suggest for epizoic fauna on *Pinna bicolor*? There are inherent difficulties in comparing communities of various marine and estuarine areas. Generalisations from one area to another are often of limited value beyond the broad observation that marine dominated sites generally have more species than estuarine sites (Collett et al 1984). Accepting this limitation it can nevertheless be seen that the total number of species found in the present study (160) is within the range of species number recorded in several studies of eastern Australian "estuarine" regions (Rainer & Fitzhardinge 1981; Jones et al 1986), and is comparable to the number recorded in a recent study of the intertidal mudflat fauna of the Port River estuary, Gulf St Vincent (Thomas et al 1986). About one and a half times as

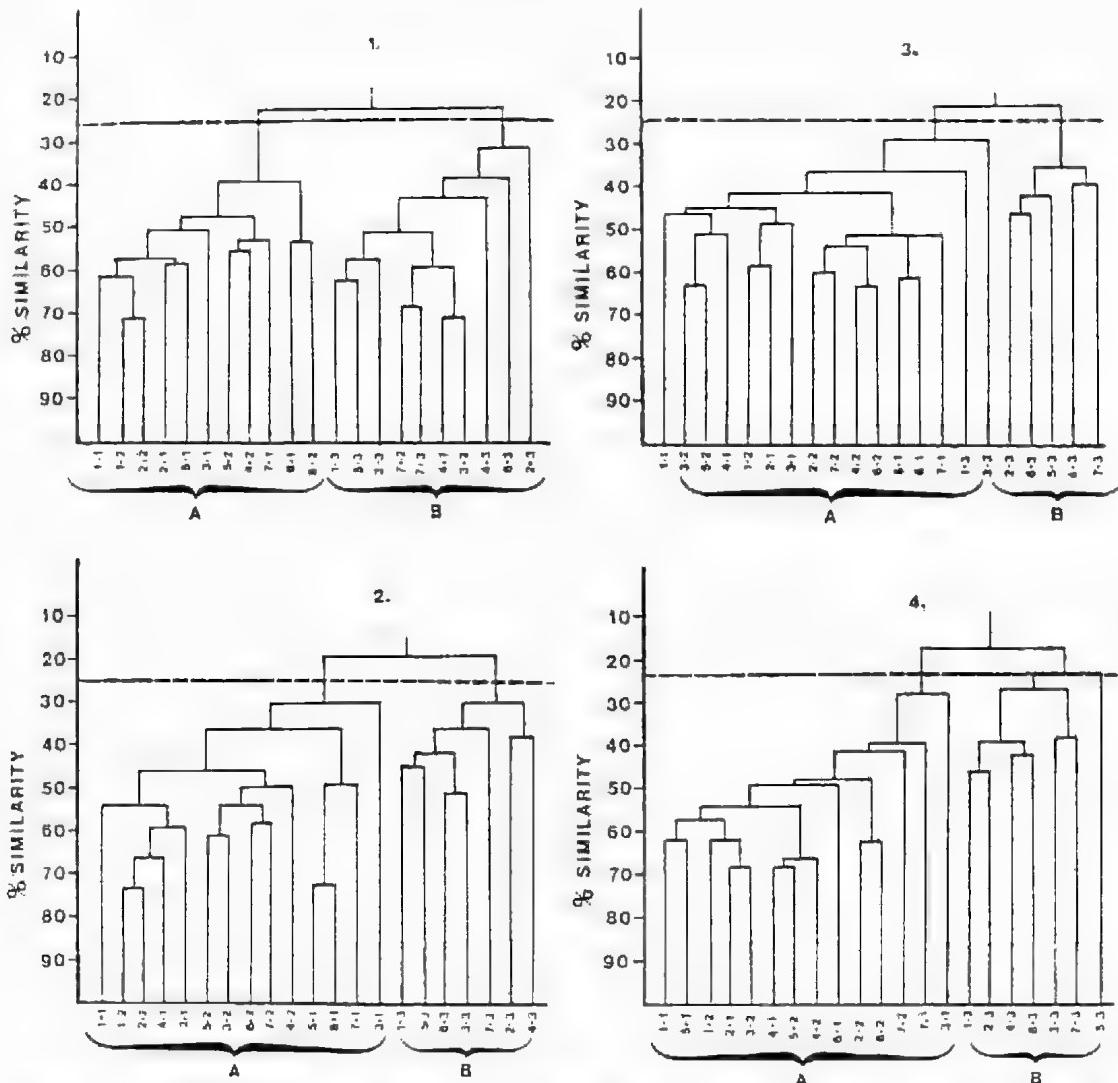


Fig. 4. Station faunal homogeneity dendograms. (1) winter 1982, (2) summer 1983, (3) summer 1986, (4) winter 1986.

many species are recorded in the present study as were recorded by Kin hill (1987)³ for intertidal mud-flats about 50 km further south in Spencer Gulf where salinities are four to five lower (Nunes & Lennon 1986). Kin hill (1987)³ did not sample at the seagrass fringe (D Evans pers. comm.). Disregarding the 38% of the total number of species which are exclusive to the seagrass fringe in the present study leaves a species number very similar to that found by Kin hill (1987)³. Therefore this study provides no evidence of species impoverishment in the intertidal zone, related to high salinity or other environmental factors characteristic of the area.

Natural variations in the intertidal communities of northern Spencer Gulf

For a baseline study to be of use in post development monitoring an understanding of natural variations in the species matrix is necessary. The faunal homogeneity dendograms for both stations and tidal zones demonstrate the consistent relationship between the mid intertidal and low intertidal communities over several seasons. Between 1982 and 1986 the common core species characterising these two habitats remained constant (Table 2). Perhaps surprisingly no seasonal pattern emerged from the intersurvey comparisons. The over-riding pattern

which showed for both habitats was the trend for sequential subgrouping of surveys, with survey faunas within each of the two habitats showing high similarity grouping at the 60%–70% similarity level in each case. Sequential grouping of survey faunas does not appear to be unusual. Saenger *et al* (1980) interpreted such a pattern as demonstrating progressive recolonisation following environmental disturbance. Buchanan *et al* (1974, 1978), however, observed similar sequential subgrouping of survey faunas from undisturbed marine environments and interpreted this pattern as indicating a more or less continual change in the presence and abundance of occasional or rare species while the core species remain relatively constant. Given the

overall similarity in survey faunas over time this seems the most likely explanation here. The slightly lower intersurvey similarities of the low intertidal communities, compared to those of the mid intertidal communities, is a consequence of the fact that the former are characterised by more rare or occasional species.

Monitoring for changes associated with environmental disturbance

Changes in estuarine faunas in response to organic or thermal disturbance have been well documented (Gray 1976; Parker 1980; Bamber & Spencer 1984; Thomas *et al* 1986). In particular, in the negative estuary of the Port River, Gulf St

TABLE 2. Common species of the intertidal fauna of Northern Spencer Gulf, determined by reference to constancy, and abundance rank scores (Hailstone 1976). Note that the top 40 species ranked in this table includes all 21 species^a which would be selected on Field *et al*'s (1982) arbitrary cutoff for dominant species, namely species which contribute 4% or more to the total population of any one survey.

RANK	CODE (Refer Fig. 6)	SPECIES	% ABUNDANCE	% CONSTANCY
1	W1	<i>Oliganereis edmondsi</i>	10.2	73.5
2	W3	<i>Nephlys australiensis</i>	7.7	95.1
3	B7	<i>Brachidontes erosus</i>	36.8	65.9
4	B1	<i>Tellina deltoidalis</i>	3.0	73.0
5	B15	<i>Nassarius pauperatus</i>	2.2	67.6
6*	C4	<i>Paguristes frontalis</i>	2.3	62.2
7	B13	<i>Bauillaria diemenensis</i>	3.9	47.0
8	B4	<i>Katelysia scalarina</i>	2.0	56.7
9	C7	<i>Elminius modestus</i>	4.3	33.0
10	W6	<i>Scoloplos cylindrifer</i>	1.7	49.2
11	W2	<i>Neanthes vaalii</i>	1.8	45.9
12	B9	<i>Monodonta constricta</i>	0.95	34.0
13	C2	<i>Callianassa ceramicus</i>	0.8	53.5
14	B3	<i>Salinator fragilis</i>	3.7	23.8
14*	W7	<i>Cirriformia filigerá</i>	0.95	34.0
16	C32	<i>Balanus amphitrite</i>	4.6	20.5
17*	W10	<i>Borantiolla leptae</i>	0.9	28.1
18*	C18	<i>Apsuedes australis</i>	0.9	23.8
19*	W30	<i>Nemertean spp</i>	0.35	34.6
20	W11	<i>Nereis triangularis</i>	0.55	24.3
20*	B5	<i>Nassarius burchardi</i>	0.5	28.1
22*	W15	<i>Maldanidae</i>	0.5	26.5
23	W9	<i>Marphysa sp</i>	0.37	28.1
24	W19	<i>Terebellinae 1</i>	0.6	17.8
24	W22	<i>Lysilla aphelae</i>	0.5	22.2
26	C14	<i>Crangon socialis</i>	0.28	23.8
27	C9	<i>Philyra laevis</i>	0.26	23.8
28	B2	<i>Laternula recta</i>	0.21	23.8
29	B26	<i>Asteracmea sp 1</i>	0.3	20.5
30	B11	<i>Bauillaria estuarina</i>	0.7	9.7
31	B12	<i>Bedeva paivae</i>	0.17	17.8
32	X5	<i>Anthothoe albocincta</i>	0.2	15.1
33*	W33	<i>Eupolymlia nebulosa</i>	0.4	9.7
33	W20	<i>Sireblosoma sp</i>	0.24	13.0
35	B14	<i>Katelysia peronii</i>	0.14	15.7
36*	W38	<i>Golfingia m adelaideensis</i>	0.14	13.5
37*	B35	<i>Electroma georgiana</i>	0.2	10.8
38*	B20	<i>Australiotia densilineata</i>	0.5	7.6
38*	W34	<i>Schistomerengos sp</i>	0.12	15.1
40*	W12	<i>Leitoscoloplos normalis</i>	0.15	10.8

* Most common species in the low intertidal zone Group B1 Fig. 6.

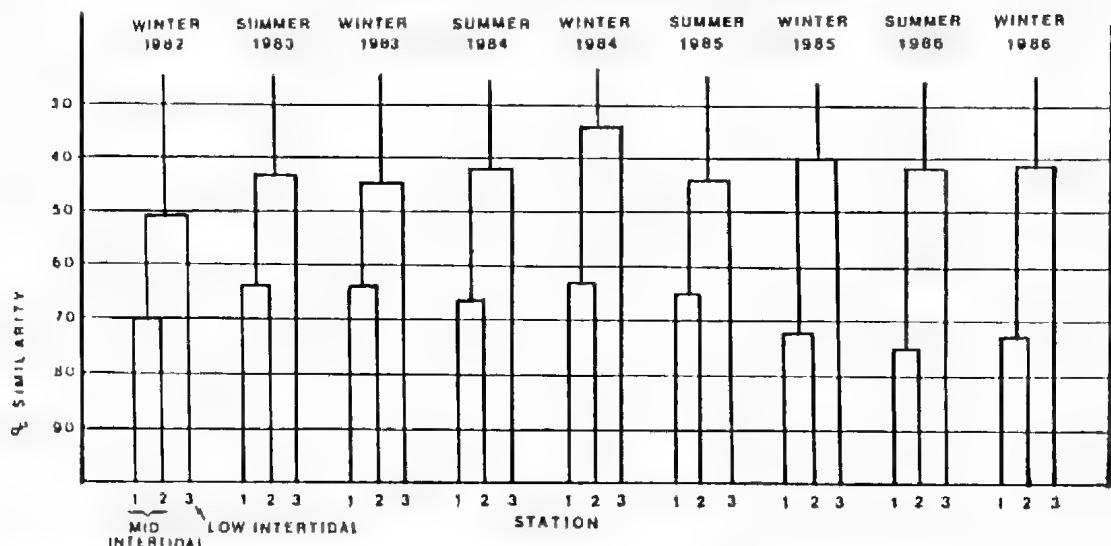


Fig. 5. Faunal homogeneity dendograms with respect to tidal zones for all surveys, 1982–1986.

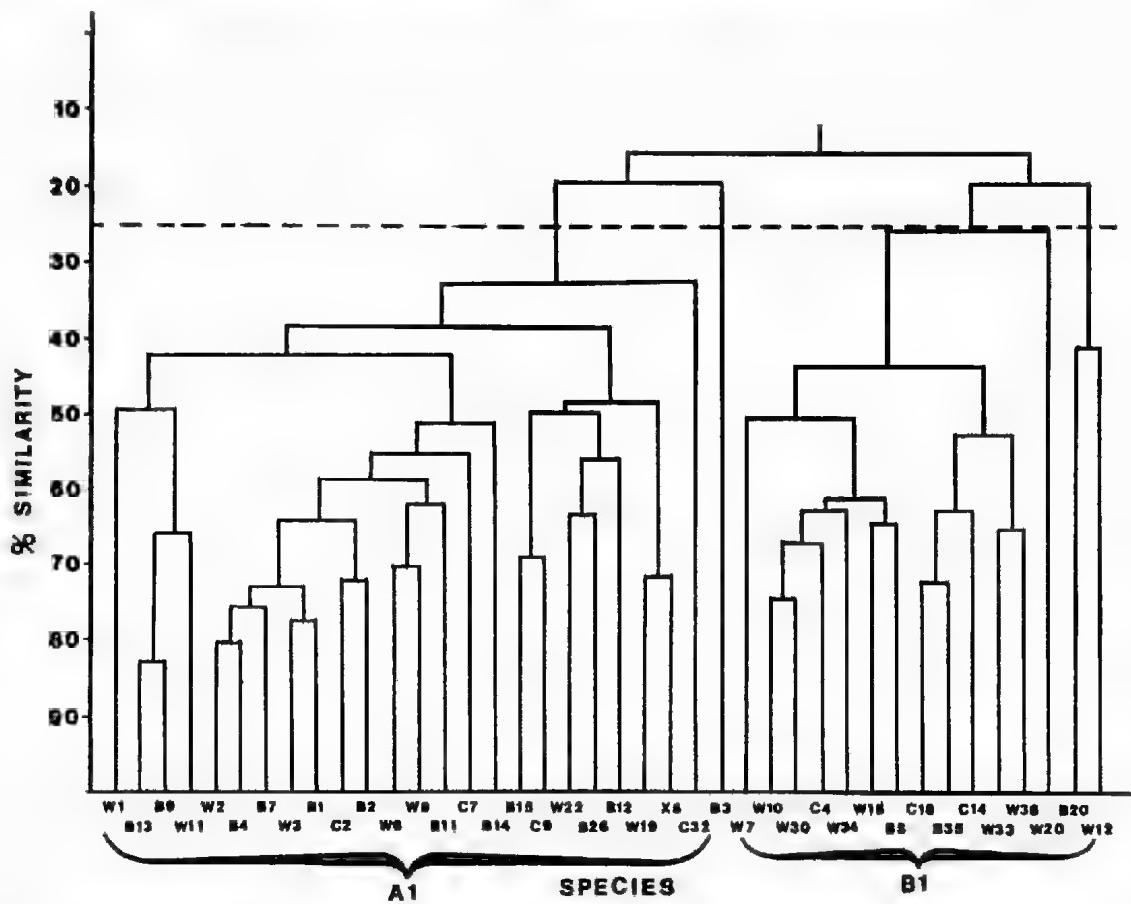


Fig. 6. Species homogeneity dendrogram determined on non transformed data for the 40 most common species for the period 1982–1986 as determined by average rank scores assigned as in Hailstone (1976).

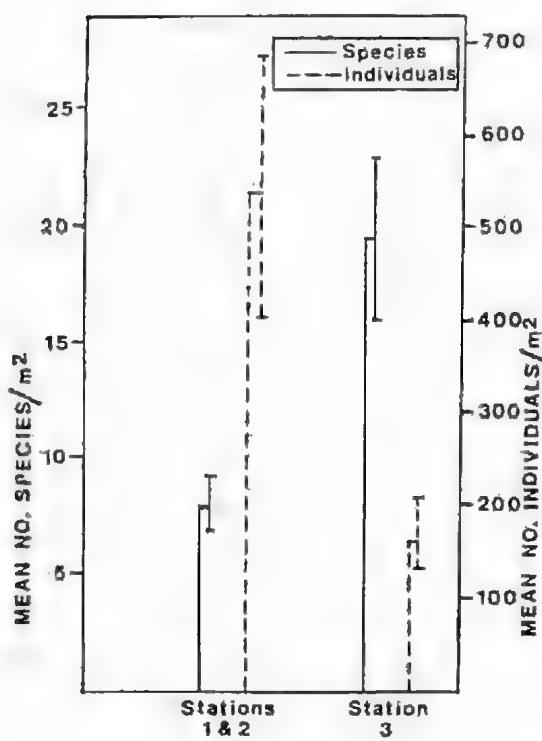


Fig. 7. Comparison of numbers of species/m² and numbers of individuals/m² for mid intertidal stations 1 and 2, and for low intertidal stations 3's.

Vincent, Thomas *et al* (1986) describe responses of intertidal communities to progressive increase of thermal discharge from Torrens Island Power Station. These include suppression or elimination of populations of bivalve mollusc and worm species characteristic of undisturbed regions, and increases in populations of opportunistic worm species. Of the 120 species recorded from the Port River estuary about 50 species (40%) also contribute to the 160 species of the present study. These include several bivalve and worm species which had a negative response to thermal discharges, and which played a significant part in defining thermal perturbation in the Port River, namely the bivalves *Tellina deltoidalis*, *Katelysia scalarina* and *K. peronii*, and the worms *Nephtys australiensis*, *Neanthes vaalii* and *Scoloplos cylindrifer*. All of these species are common in the communities of the mudflats of northern Spencer Gulf, particularly in the mid intertidal zone (Table 2). The presence of these common indicator species provides the basis of a monitoring programme to detect potential thermal perturbation in northern Spencer Gulf. Any changes in abundance of these species in areas near thermal discharges will be reflected in recognisable changes to the stable faunal homogeneity rela-

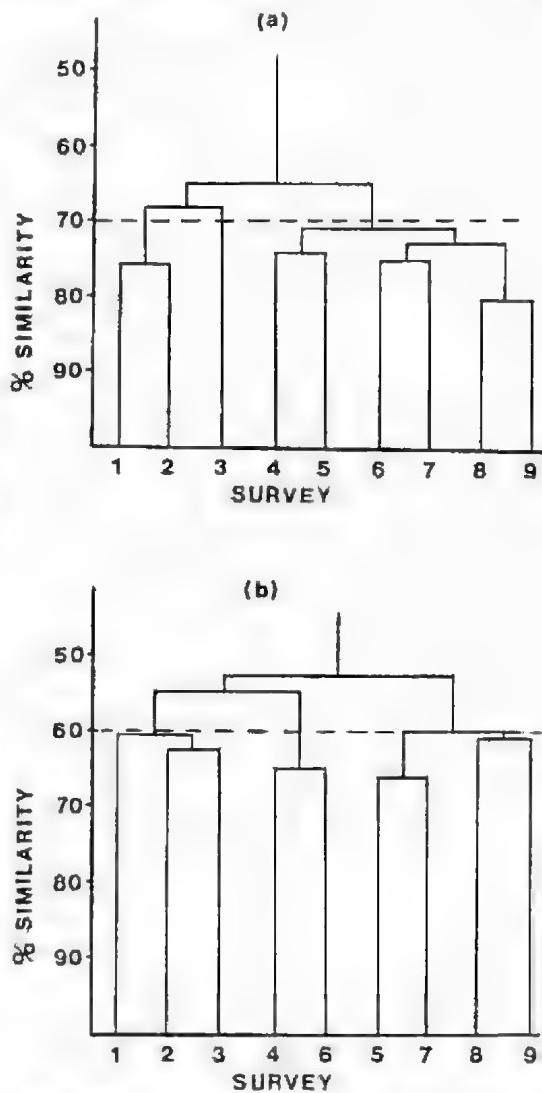


Fig. 8. Intersurvey faunal homogeneity dendograms. (a) stations 1 and 2, (b) stations 3. Survey number 1 – winter 1982, 2 – summer 1983, 3 – winter 1983, 4 – summer 1984, 5 – winter 1984, 6 – summer 1985, 7 – winter 1985, 8 – summer 1986, 9 – winter 1986.

tionships described in this study over the period 1982–1986. Such changes in faunal homogeneity dendrogram patterns have been clearly demonstrated by Thomas *et al* (1986) in studies of changes in the fauna of the Port River estuary with progressive increase in thermal discharge to that region. The cirratulid worm *Cirriformia filigera* is common in the low intertidal zone (Tables 1–2). Although the life history of this particular species is not well known, other members of this genus have been shown to have typical opportunistic characteristics, capable of rapid colonisation of disturbed regions

(George 1964 a,b; Thomas *et al* 1986). The archetypal opportunistic worm species *Capitella capitata* (Grassle & Grassle 1974; Gray 1976; Tsumsumi 1987) has not been recorded in the present study. It is, however, present in intertidal communities 50 km further south (Kinhill 1987), and it is not unusual for opportunistic species in disturbed regions to be immigrants from other regions (Thomas *et al* 1986). As with changes in the indicator species discussed above, any changes in populations of opportunistic worm species near the thermal discharge can be expected to noticeably alter the patterns of the faunal homogeneity dendograms, warning of potentially significant environmental perturbation. To 1986 no impact of the occasional incursions of warmed water from Thomas Play-

ford Power Station to the intertidal zone, and the initial discharge from the Northern Power Station (from summer 1985) can be discerned from community relationships described in the present study.

Acknowledgments

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**ROTIFERA FROM AUSTRALIAN INLAND WATERS.
III. EUCHLANIDAE, MYTILINIDAE AND TRICHOTRIIDAE
(ROTIFERA:MONOGONONTA)**

BY W. KOSTE & R. J. SHIEL†*

Summary

Diagnostic keys are given to the Australian representatives of the Rotifera: Monogononta in the families Euchlanidae (*Manfreedium*, *Diplois*, *Dipleuchlanis*, *Tripleuchlanis*, *Euchlanis*), Mytilinidae (*Mytilina*, *Lophocharis*) and Trichotriidae (*Wolga*, *Macrochaetus*, *Trichotria*). All species known from Australian inland waters are described and figured, as are some widely distributed taxa not yet recorded from the continent. Distribution data and ecological information also are given.

KEY WORDS: Rotifera, Euchlanidae, Mytilinidae, Trichotriidae, Australia, taxonomic revision.

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KEY WORDS: Rotifera, Euchlanidae, Mytilinidae, Trichotriidae, Australia, taxonomic revision.

Introduction

The families of Rotifera:Monogononta considered in this part of our review of the Australian species (see Koste & Shiel 1986b, 1987b) commonly are encountered in the shallow littoral zones of billabongs or vegetated lake margins (cf. Koste 1981, Tait *et al.* 1984, Koste & Shiel 1986a, 1987a, Koste *et al.* 1988). Some species, e.g. *Euchlanis dilatata* and related forms, are known to become planktonic in eutrophic waters during cyanobacterial blooms (Ruttner-Kolisko 1974). This species occurs seasonally in the lower R. Murray, S. Aust. (Shiel *et al.* 1982). Otherwise, species of the Euchlanidae (*Manfredium*, *Diplois*, *Dipleuchlanis*, *Tripleuchlanis*, *Euchlanis*), Mytilinidae (*Mytilina*, *Lophocharis*) and Trichotriidae (*Walga*, *Macrochaetus*, *Trichotria*) generally are benthic or epiphytic in habit, and occur in open water of lakes, reservoirs or rivers only as incursion species during seasonal flushing flows.

Most of the 35 taxa recorded in the three families were collected as such incidental incursions into the limnetic region of billabongs. It is likely that more taxa remain to be described, particularly endemic species, because our initial sampling program was directed at the planktonic community and the sampling bias has "undersampled" the preferred habitat of these littoral rotifers. Only four endemic species are known in the three families, one mytilinid (*Lophocharis curvata*) and three trichotriids (*Trichotria pseudocurta* and *T. buckneri* from Tasmania, and *Macrochaetus danneeli*, from the N.T.). In contrast, about 25% of the taxa in the Epiphaniidae and Brachionidae (Koste & Shiel

1987b), true limnetic species (and therefore more intensively sampled), apparently are endemic.

All known Australian representatives of the three families are described and figured, and diagnostic keys are provided to enable identification to species. Widely-distributed taxa not yet recorded from Australia, but which are likely to be found here, are included in some genera. The format follows that of earlier papers; dichotomous keys are followed by individual species' descriptions and known Australian records. Relative abundance from >2000 collections is indicated by: "rare" (fewer than ten records, "uncommon" (10–30 localities) and "common" (more than 30 widely dispersed localities). Brief ecological data are included where available, generally in the sequence: temperature (°C), pH, dissolved oxygen (DO, mg l⁻¹), conductivity (K_{1a}, µS cm⁻¹) and turbidity (nephelometric turbidity units (NTU)).

To minimise the citation of previous references to the rotifer families reviewed here, early Australian references which are included in Shiel & Koste (1979) are not repeated, nor are the majority of European references, which are included, for example, in the reviews of Hulson & Gosse (1886, 1889), Weber (1898), Voigt (1957), Bartos (1959), Rudescu (1960), Kutikova (1970) and Koste (1978). A more detailed treatment of the Rotifera outside Australia is given by these authors.

Family Euchlanidae Bartos

The following genera were integrated by Remane (1929–1933) in the subfamily Brachionidae. A special family was erected by Bartos (1959), later accepted by Kutikova (1970) and Koste (1978). With the exception of *Manfredium* the genera are characterized by a lorica with plates which are connected with sulci, a segmented foot, more or less elongated toes, a corona of the same type (*Euchlanis*-type, Fig. 3d) and malleate trophi (Fig. 2:2b,3).

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Key to genera of the Family Euchlanidae

1. Lorica thin, without lateral sulci, long toes
..... *Manfreodium* Gallagher
2. Lorica rigid, with dorsal and sometimes ventral plates
 - 2(1). Lorica composed of three plates; dorsal divided, separated by sulci..... *Diplois* Gosse
 - 2(2). Dorsal plate arched, concave, narrower than arched ventral plate..... *Dipleuchlanis* Beauchamp
 3. Dorsal plate arched, convex or triangular..... *Euchlanis* Ehrenberg
- 4(3). Dorsal and ventral plates nearly of same size, connected by a lateral double longitudinal membrane within a stiff projection.... *Tripleuchlanis* Myers
With and without lateral longitudinal sulci..... *Euchlanis* Ehrenberg

Genus *Manfreodium* Gallagher

Eudactylota Manfredi, 1927, p. 58 (non Walsingham, 1911).

Beauchampiella Remane, 1929, p. 107.

Eudactylota Manfredi, 1927 is a junior homonym of *Eudactylota* Walsingham, 1911 (Lepidoptera). *Beauchampiella* Remane, 1929 is a *nomen nudum* under articles 12 and 16 of the International Code of Zoological Nomenclature (name published without description, definition). *Manfreodium* was proposed by Gallagher (1957) to replace *Eudactylota* Manfredi. There is a single species, *Manfreodium eudactylotum*.

Manfreodium eudactylotum* (Gosse)*FIG. 1**

Scardium eudactylotum Gosse In Hudson & Gosse, 1886, p. 74, Fig. 21:4.

Eudactylota eudactylotum (Gosse) Manfredi, 1927, p. 58.
Beauchampiella eudactylotia (Gosse) Remane, 1929, p. 107.

Manfreodium eudactylotum (Gosse) after Gallagher, 1957, p. 183.

Diagnosis: Body pear-shaped with soft, transparent cuticle; head small; foot with two longer segments; toes long, rod-shaped; striated muscles visible in caudal part of body and foot; mastax trifoliated, trophi malleate (Fig. 1:f); oesophagus with small paired glands; large red cerebral eye; resting egg with fine hairs (Fig. 1:e).

Length: 420–760 μm , foot 80–110 μm , toes 275–320 μm , trophi 25 μm , longest uncus tooth 12 μm , manubrium 18 μm .

Distribution: Cosmopolitan, pancontinental in Australia, rare. Warm stenotherm, 11.5–17.0°C, pH 4.8–6.5, conductivity to 1600 $\mu\text{s cm}^{-1}$. The rotifer may swim between water plants, also jumps by flicking the toes.

Literature: Koste 1978, 1981; Ridder 1981; Koste & Robertson 1983; Koste & Shiel 1987a

Genus *Diplois* Gosse

Diplois Gosse In Hudson & Gosse, 1886, Vol. 2, p. 86.

Diplois daviesiae* Gosse*FIG. 2:1**

Diplois daviesiae Gosse In Hudson and Gosse, 1886, Vol. 2, p. 87, Fig. 24:3.

D. phlegrea Ircio, 1910, p. 301.

D. sculpturata Daday, 1897, p. 135 (from New Guinea).

Diagnosis: Lorica with three plates; arched dorsal plate divided longitudinally by sulcus; lateral sulci small; foot three-segmented; toes thin; lorica surface smooth, flexible; head short, broad; eye with lens; oesophagus short; stomach compact; gastric glands large.

Length: to 500 μm , width 225 μm , toes 100 μm .

Distribution: May be cosmopolitan in the benthic of freshwater *Sphagnum* pools. Not yet recorded from the Neotropics. Not recorded in this study, but there is an early record from Qld (Thorpe 1887).

Genus *Dipleuchlanis* Beauchamp

Dipleuchlanis Beauchamp, 1910, p. 122.

Dorsal plate narrower than ventral plate; foot three-segmented; toes more or less long, rod-shaped with tapering points occasionally swollen terminally; rami points with minute comb (Fig. 2:2b); uncus with 7–10 teeth; gastric glands long in younger individuals, broader and lobed in adult; red cerebral eye. Two variants of a single species (*D. propatula*) are known from Australia; individuals can be discriminated by toe structure. *D. propatula* has toes without a swelling before the points, whereas *D. propatula macrodactyla* has toes with a swelling.

Dipleuchlanis propatula propatula* (Gosse)*FIG. 2:2a-f**

Diplois propatula Gosse In Hudson & Gosse, 1886, p. 87, Fig. 24:2.

Dipleuchlanis propatula (Gosse) after Beauchamp, 1910, p. 122.

Diagnosis: Caudal part of dorsal plate sometimes stretched to rounded point and reaches nearly to end of ventral plate; toes tapering to short point.

Length: 338–508 μm , lorica length to 500 μm , width to 200 μm ; toes 70–110 μm .

Distribution: Cosmopolitan in littoral, sometimes occurs in plankton of ponds or billabongs. Rare, Vic, N.T. Warm stenotherm, pH 4.5–6.4, also in O₂-poor waters on the surface of mud.

Literature: Koste 1978, 1981.

Dipleuchlanis propatula macrodactyla* (Hauer)*FIG. 2:2g**

Dipleuchlanis macrodactyla Hauer, 1965, p. 351.

Dipleuchlanis propatula f. macrodactyla (Hauer) after Koste, 1978, p. 145.

Diagnosis: Caudal part of dorsal lorica with short paired cuticular projections; toes long.

Length: 128–244 μm , width 69–212 μm , toes 112–168 μm .

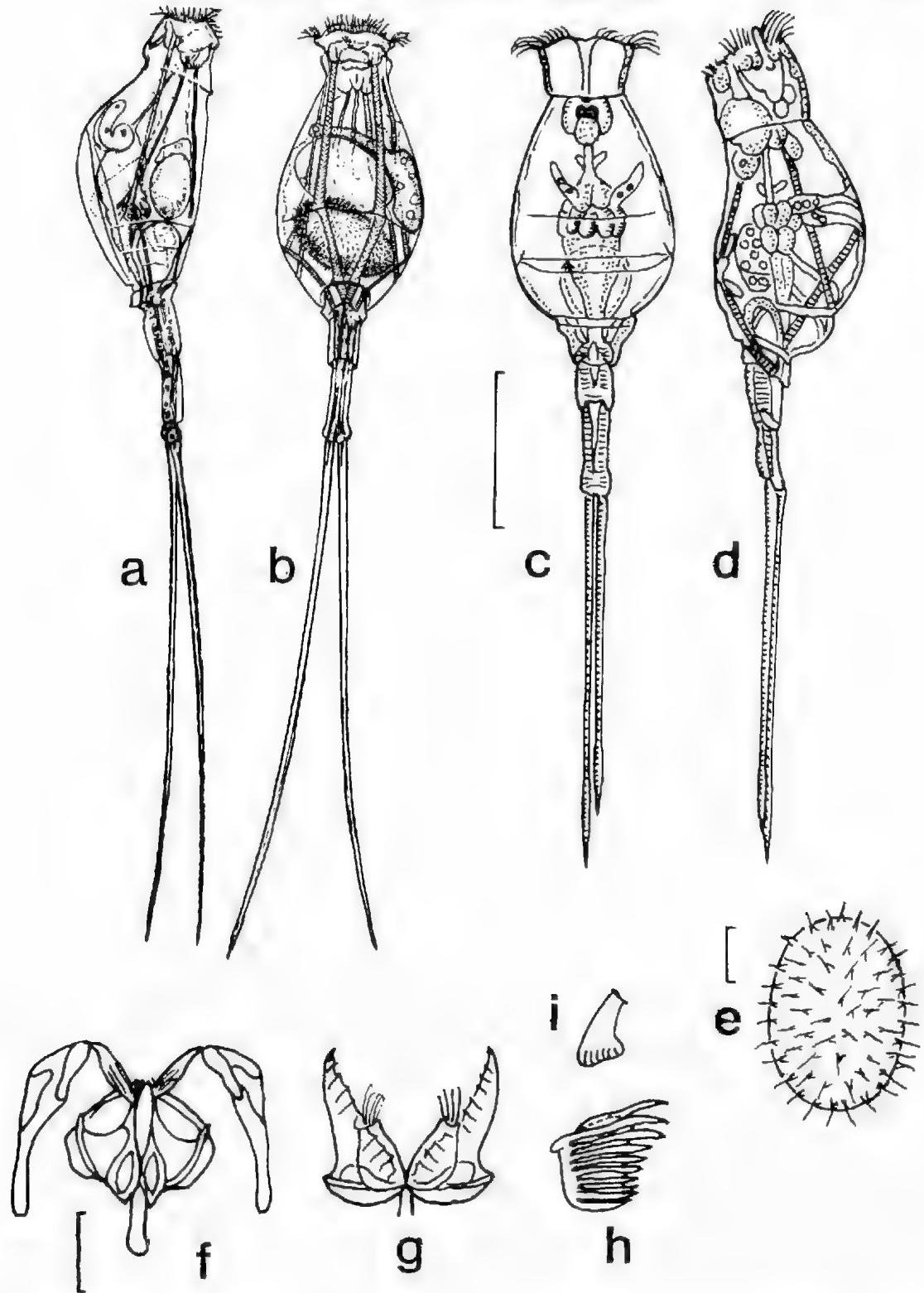


Fig 1: *Manfredium eudactylotum* (Gosse): (a) lateral; (b) ventral; (c) dorsal; (d) lateral; (e) resting egg; (f) trophi; (g) opened rami; (h) uncus; (i) fulcrum. Fig. 1a-d, f-i after Wulfert (1940); e after Koste (1978). Scales lines, top 100 μm (a-d); lower right 20 μm (e); lower left 10 μm (f-i).

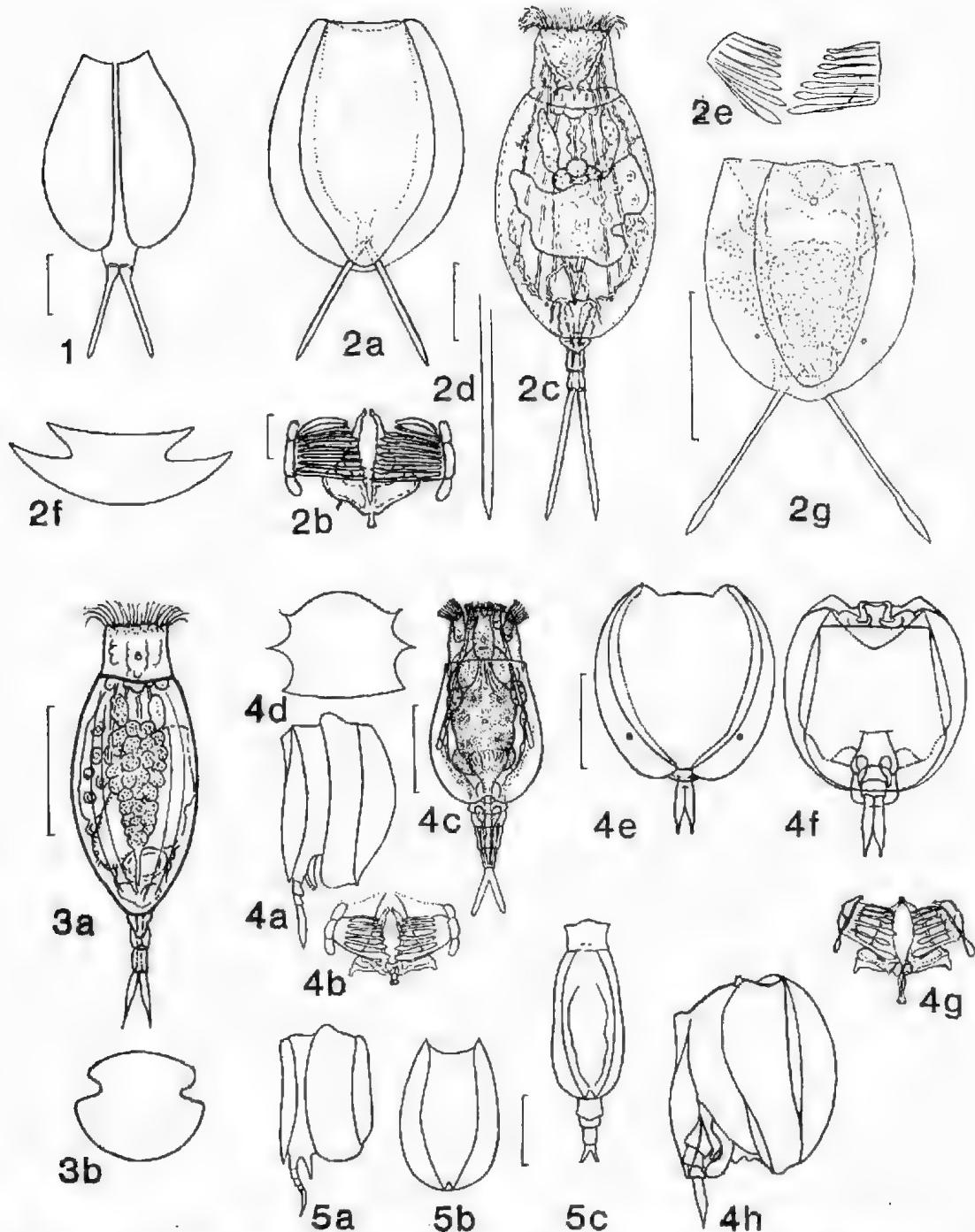


Fig. 2: 1, *Diplois daviesiae* Gosse, dorsal. 2, *Dipleuchlanis propatula propatula* (Gosse): (a) dorsal; (b) trophi; (c) ventral, swimming; (d) toe; (e) unci; (f) cross-section; (g) *D. propatula macrodactyla* (Hauer), dorsal. 3, *D. elegans* (Wierzejski): (a) dorsal; (b) lorica cross-section (cf. *D. propatula*). 4, *Tripleuchlanis plicata plicata* (Levander): (a) lateral; (b) trophont; (c) swimming; (d) cross-section; (e) dorsal; (f) ventral; (g) trophi, apical; (h) lateral. 5, *T. plicata razelni* Rodewald: (a) lateral, (b) dorsal, swimming; (c) ventral. Fig. 2:1, after Weber (1898); 2a, b, f, 3a-d, after Myers (1930); 2c, d, 3, after Fadecew (1924); 2g, 3e-g, after Hauer (1965); 5a-c, after Rodewald-Rudescu (1960). Scale lines Fig. 2:1-4, 100 µm (adult lorica each number group); 5, 50 µm; 2b, 4b, g, 10 µm.

Distribution: Pantropical. N.T., Vic. Water to 32°C, pH 5.4–6.5.

Literature: Myers 1930; Hauer 1965; Koste 1974, 1981; Berzins 1982.

Doubtful or insufficiently described species:

Dipleuchlanis elegans (Wierzejski, 1893) = *Euchlanis propatula elegans* (Fig. 2:3) according to Beauchamp, 1910, p. 122.

Dipleuchlanis conradi Evans, 1947, p. 179, Fig. 5.
Dipleuchlanis paludosa Hauer, 1936, p. 139, Fig. 2:12.

Genus *Tripleuchlanis* Myers

Tripleuchlanis Myers, 1930 p. 379.

Lorica ovoid in shape, truncate in front, smoothly-rounded caudally; dorsal and ventral plate nearly of same size, connected by pair of lateral longitudinal sulci. Longitudinal flange of stiffened cuticle extending for entire length between each, giving bellows-like appearance to cross-section. Foot three-jointed, guarded by shield-like process extending downwards from median longitudinal flange; toes short ending in abrupt points; mastax of modified malleate type (Fig. 2:4h); six club-shaped teeth on each uncus; rami triangular with minute denticulate combs at inside of tip; double cerebral eye. A single species, *T. plicata*, with a doubtful variant (*T. plicata* f. *razelmi* (Fig. 2:5)) from Romania distinguished on the basis of an elongated dorsal plate, caudally with a rounded notch (Rodewald 1940:88).

Tripleuchlanis plicata (Levander)

FIG. 2:4

Euchlanis plicata Levander, 1894 p. 48.

Tripleuchlanis plicata (Levander) after Myers, 1930, p. 379.

Diagnosis: Lorica stout; foot glands and reservoirs elongated; retrocerebral organ small.

Length: 250–270 µm, dorsal plate 90–130 µm, ventral plate 100–115 µm, toes 25–37 µm.

Distribution: Cosmopolitan; rare in fresh-, more in brackish and marine waters, also in warm springs. Qld, Vic.

Literature: Hauer 1925, Koste 1978.

Genus *Euchlanis* Ehrenberg

Euchlumis Ehrenberg, 1832, p. 13.

Lorica transparent with oval or ovate outline; dorsal plate arched, convex, sometimes with median keel or lateral wings, larger than ventral plate, variable in height and shape; ventral plate caudally somewhat indented, nearly flat. Two plates connected by thin, flexible cuticle forming longitudinal sulci. Foot with two or three joints; toes long or short, sword-shaped or parallel-sided, with sharp tips. Paired long setae situated on dorso-distal portion of foot-segments (Fig. 3a:ss). Corona of

family type (Fig. 3d); long sensory bristles and cilia in tufts and solitary on apical field. Trophi (Fig. 3e, f) modified malleate; fulcrum (Fig. 3f:fr) broad, pointed rami (ra) with and without minute comb; uncus with main and variable number of accessory teeth. Brain with large cerebral eye (Fig. 3b ey) behind large mastax. Large retrocerebral organ present (Fig. 3b:re), with subcerebral glands. Dorsal antenna large; lateral antenna (Fig. 3b:la) with sensillae tufts on small tubules. Stomach sometimes with sacculi but not constant between species. Excretory organ with large contractile bladder (Fig. 3a,b:bl). Vitellarium with eight large nuclei. Male thinly loricate (Fig. 3l:m) with reduced alimentary tract; protonephridia present. Foot with two to three joints; two long sensory bristles on terminal joint. Toes short. Dark resting eggs may be attached to plants (Fig. 3h,j).

Euchlanis species are littoral rotifers living among aquatic plants, but in the pelagic they occur in eutrophic lakes and ponds at *Cyanophyta maxima*, especially of *Gloeotrichia*, the main food of *Euchlanis dilatata* (Ruttner-Kolisko 1974). Other foods consists of diatoms, desmids, other algae and detritus.

The taxonomy of the different species is difficult; even within the same population lorica shape and cross-section is variable. The shape of the anterior margin of both plates is of little value in the determination. Most useful is trophi structure, which is species-specific. *Euchlanis* should not be pressed by a coverslip. See for example *E. menetii* cross-sections and the different forms of *E. dilatata*.

Key to Species of the Genus *Euchlanis*

1. Cross section of lorica more or less arched to semi-circular 2
2. Cross section of lorica triangular, dorsal plate with high keel 10
- 2(1). Posterior edge of dorsal lorica with distinct notch or embayment (cf. Fig. 7:1k; Fig. 8:2a) 6
Notch absent, or only shallow emargination (cf. Figs. 4:3b, 6:3) 3
- 3(2). Ventral plate present 4
Venter membranous or rudimentary 5
- 4(3). Ventral plate ca. $\frac{1}{2}$ dorsal plate width; wing-like lateral expansions of dorsal lorica margin (Fig. 4:3b) *E. olata* Voronkov
Ventral plate ca. $\frac{1}{3}$ dorsal plate width, constricted at posterior end; no expanded margins (Fig. 6:3) *E. lyra* Hudson
- 5(3). Lateral constrictions in medial dorsal lorica; flanged lateral margins (Fig. 8:3) *E. pyriformis* Gosse
Dorsal lorica not constricted, lateral margin not flanged (Figs 4:3, 4:4) *E. deflexa* Gosse
- 6(2). Cuticular shield-like process just below caudal part of dorsal plate (Fig. 7:10) *E. menetii* Myers
Shield-like process lacking 7
- 7(6). Ventral plate rudimentary; longitudinal sulci absent; toes very long (>100 µm), slender (Fig. 4:2) *E. cypridia* Myers
Ventral plate well developed 8

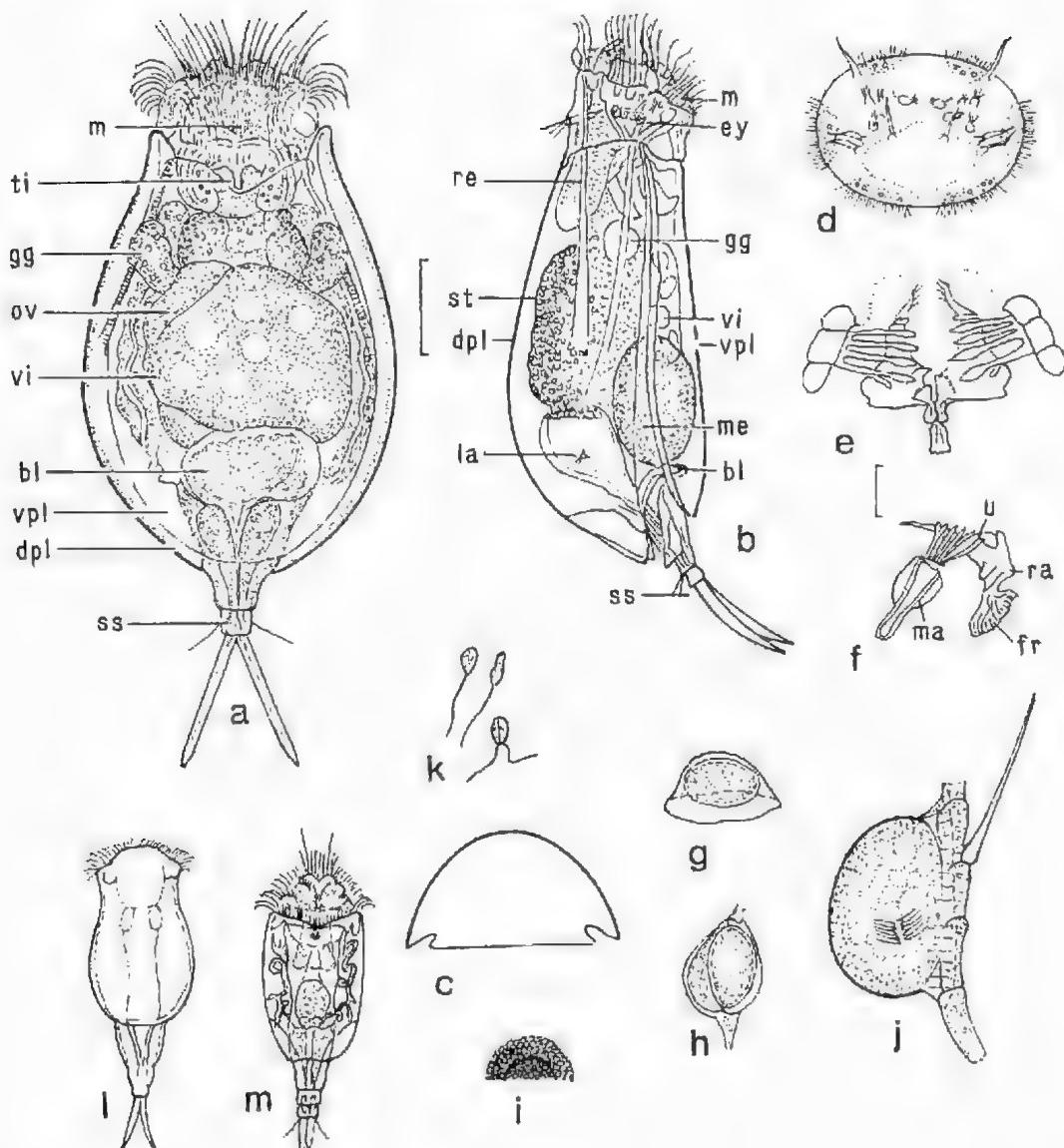


Fig. 3: *Euchlanis dilatata dilatata* Ehrenberg: (a) ventral; (b) lateral; (c) cross-section; (d) apical field; (e) trophont; (f) trophi, lateral; (g) *E. triquetra*, amictic egg; (h) mictic egg; (i) *E. dilatata*, mictic egg; (j) subitaneous egg; (k) sperm; (l) male; (m) *E. deflexa*, male. (Key to a,b: bl = bladder; dpl = dorsal plate of lorica; ey = eye; gg = gastric glands; la = lateral antenna; m = mouth; me = membrane; ov = ovary; re = retrocerebral sac; st = stomach; ss = sensory bristles; vi = vitellarium; vpl = ventral plate of lorica. Key to f: ma = manubrium; fr = fulcrum; ra = ramus; u = uncus. Fig. 3a, c, j, after Koste (1978); b, after Beauchamp (1965); d, after Remane (1933); e, after Hauer (1930); f, after Voigt (1957); g, h, after Wessenberg-Lund (1929); i, after Kozar (1914); k, after Ruttner-Kolisko (1972); l, after Wulfert (1956); m, after Leissling (1924). Scales lines, top, a-d, g-m, 50 µm; e, f, 10 µm.)

8(7). Dorsal lorica with winglike lateral extensions deflected ventrally at tips (Fig. 8:2)*E. phryne* Myers
No lateral extensions of dorsal lorica. 9

9(8). Foot and toes slender; toes $\frac{1}{3}$ length of dorsal plate, blade-like, fusiform (Fig. 5:1b)*E. dilatata* Ehrenberg
Foot and toes stout; toes $\frac{1}{4}$ length of dorsal plate

toes dilated distally for $\frac{1}{3}$ length and constrict to acute points (Fig. 8:1).....*E. orophia* Gosse
10(1)Ventral plate completely developed, lateral sulci present (Fig. 6:1).....*E. incisa* Carlin
Ventral plate reduced to thin hyaline membrane; wide dorsal plate flanges (Fig. 8:1c-e).....*E. triquetra* Ehrenberg

Euchlanis alata Voronkov

FIG. 4:1

Euchlanis alata Voronkov, 1912, p. 210, Figs 2,3.

Diagnosis: Shape of body ovoid; dorsal plate without terminal notch or embayment, but may have lateral wing-like extensions (see Fig. 4:1b, d). Wingless individuals easily mistaken for *E. lyra* or *E. deflexa*. Intermediate forms common. Ventral plate elongate, relatively narrow, but without constriction before end as in *E. lyra*. Foot two-segmented and robust; toes stout and fusiform. Tips of rami incurved with pair of finely denticulate combs; four stout teeth in each uncus with several accessory teeth.

Length of dorsal plate 260–360 µm; ventral plate width 102–156 µm; toes 70–98 µm; toes width 12–20 µm.

Distribution: Nearctic and Palaearctic, in acid boreal waters, littoral and psammal. Not yet recorded from Australia.

Literature: Pejler 1962; Koste 1978; Chengalath & Koste 1983.

Euchlanis calpidia Myers

FIG. 4:2

Euchlanis calpidia Myers, 1930, p. 371, Pl. 20, Figs 1–8.

Diagnosis: Dorsal plate round, or highly domed ("obscure triradiate", i.e. helmet-like) in cross section. Middle portions of lateral edges straight or pinched, extending downward below venter; ventral plate rudimentary (cf. *E. deflexa* and *E. pyriformis*), rudiments connected with dorsal plate by flexible membrane; lateral sulci absent; foot two-jointed, slender; toes very long, parallel-sided with abrupt point. Trophi characterized by five slender paired teeth in uncus with two or three accessory teeth beside smallest. Tips of rami without minute denticulate comb. Trophi similar to those of *E. deflexa* and *E. pyriformis*. *E. calpidia* distinguished by presence of distinct posterior notch at end of dorsal plate, and by relatively long toes.

Length of dorsal plate 280–400 µm; lorica width 220–397 µm; toes 120–135 µm; toe width to 18 µm.

Distribution: Nearctic, Palaearctic (Europe to Far East). Single record from a Goulburn R. hillabong near Seymour, Vic. 22°C, pH 7.3, DO 8.0 mg l⁻¹.

Literature: Hauer 1936; Wang 1961; Kutikova 1970; Koste 1978.

Euchlanis deflexa Gosse

FIG. 4:3

Euchlanis deflexa Gosse, 1851, p. 200.

Daplidia deflexa (Gosse) in Myers 1930, p. 369, Pl. 21, Figs 1–5.

Daplidia = *Euchlanis* after Carlin, 1939, p. 16)

Diagnosis: Body resembles arc of circle in cross-section; dorsal plate ovoid, without distinct

posterior notch, sometimes with shallow emargination. Lateral edges of dorsal plate connected by flexible membrane somewhat thickened in position occupied by ventral plate in other *Euchlantis*. Posterior portion of this area more hardened as rudimentary ventral plate. No longitudinal sulci present. Foot stout and two-jointed, long setae on dorsal end of first joint; trophi with five long teeth on each uncus, clubbed at tips, with 2–3 accessory teeth; rami drawn out to long tips, minute inside combs lacking (Fig. 4:3).

Length of dorsal plate 190–350 µm, width 140–240 µm, toes 55–100 µm, toes to 15 µm wide, subtruncatus egg 180x89 µm.

Distribution: Cosmopolitan in the littoral, occasionally in the pelagic. Rare; N.S.W., Tas., Vic., W.A. There may be local variants, e.g. the Tasmanian form closely resembles *E. deflexa larga* (Fig. 4:4), described from Lake Balkasch, Siberia (Kutikova 1959). 14.0–22.0°C, pH 6.0–7.7, DO 8.0–8.6 mg l⁻¹, <70 µS cm⁻¹.

Literature: Evans 1951; Koste 1978; Shiel & Koste 1979.

Euchlanis dilatata Ehrenberg

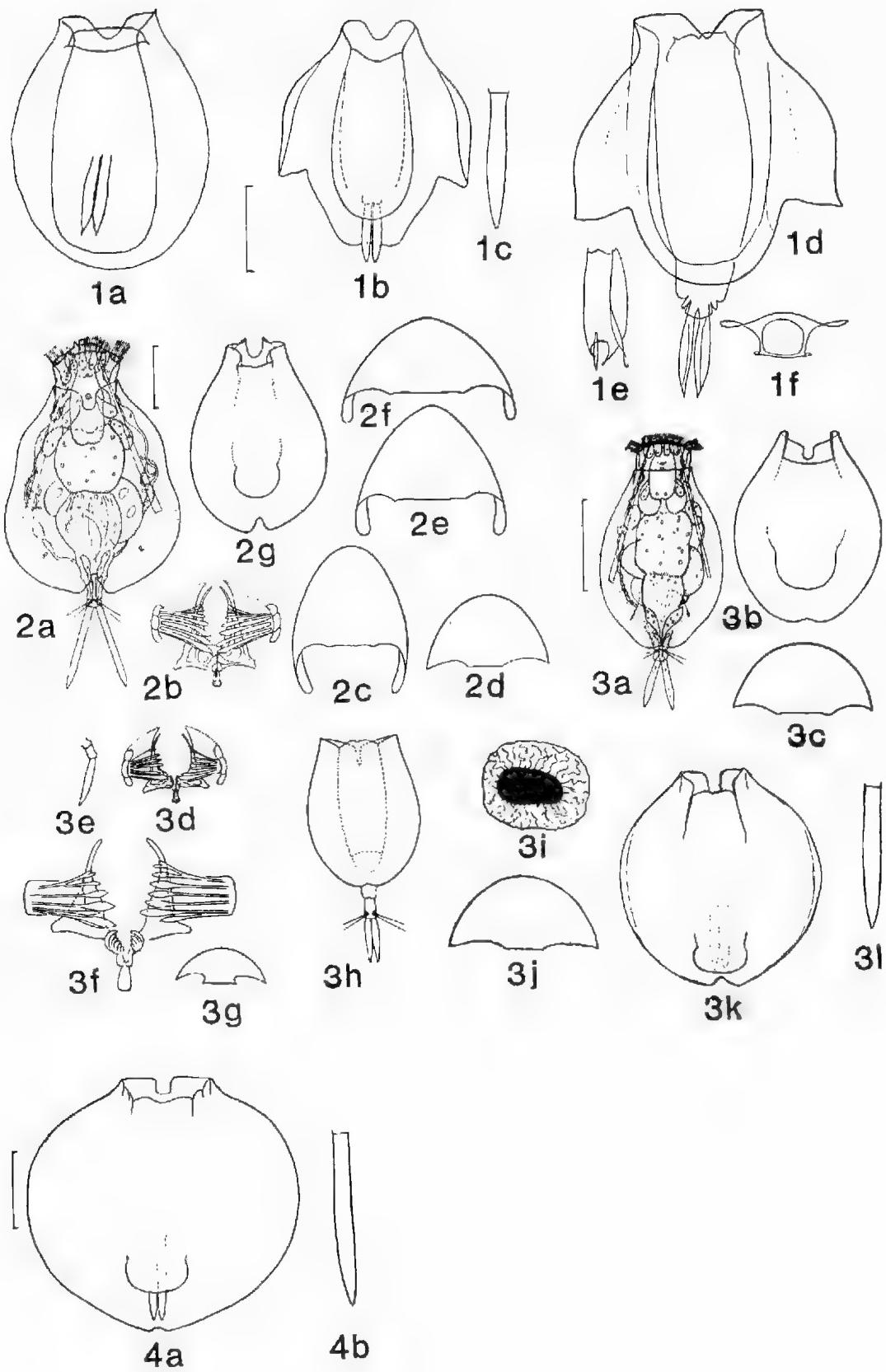
FIGS 3, 5:1

Euchlanis dilatata Ehrenberg, 1832, p. 131, Fig. 4:3.

Diagnosis: General body shape ovoid, truncate anteriorly, rounded posteriorly; dorsal plate variable in height and shape of cross-section, varying from low arc of circle to high triangle; ventral plate almost as large as dorsal; longitudinal sulci not deep and narrow (Fig. 5:1c). Posterior dorsal plate divided by deep elongate notch of variable form, cf. *f. lucksiana* (Fig. 5:4), *f. unisetata* (Fig. 5:3) or *f. larga* (Fig. 5:5). Foot slender and two-jointed; paired setae on distal margin of first segment; toes mostly parallel-sided, tapering terminally to sharp tip. Unci of trophi with four opposing teeth; ventral large teeth each have rudimentary tooth; tips of rami with inner minute denticulate comb; retrocerebral sac large (Fig. 3b:re, cf. also Fig. 5:4); brain with red eye on dorsal side.

Intraspecific forms are described exclusively according to differences in the shape of the lorica and cross sections, however research by Parise (1963) suggests that different morphological types are correlated with ecological differences. This also may apply to some distinguished species; *E. parva* Rousselet, for example, resembles *E. dilatata* and is distinguished from it by smaller size and long slender toes. All known measurements fall within the range of variation of *E. dilatata*; it is seen as an ecotype of *E. dilatata*.

Lorica length 140–320 µm, dorsal plate width 100–255 µm, ventral plate 95–172 µm, toes 50–100 µm, posterior notch 12–61 µm deep; male 115–148



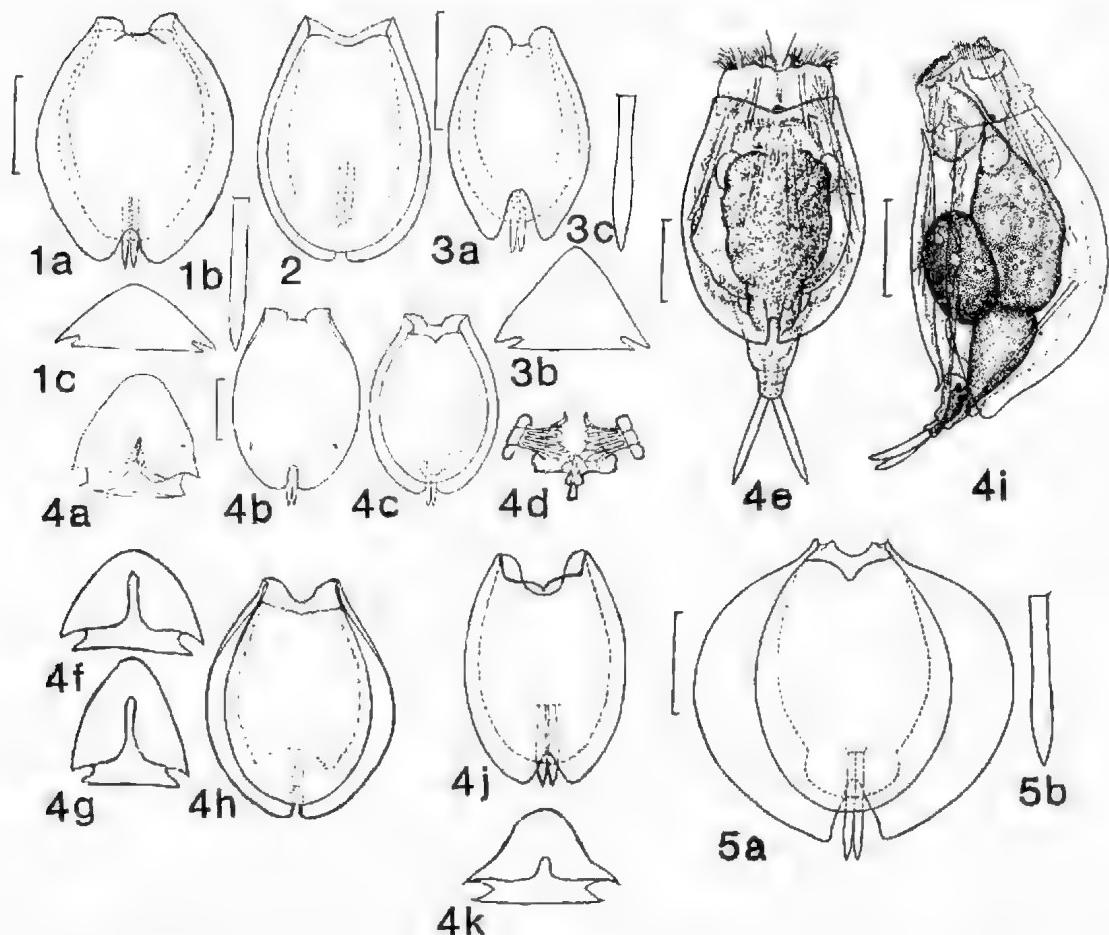


Fig 5: 1, *Euchlanis dilatata dilatata* Ehrenberg; (a) dorsal; (b) toe; (c) cross-section. . *E. dilatata macrura* (Ehrenberg); ventral. 3, *E. dilatata f. unisetata* (Leydig); (a) dorsal; (b) cross-section; (c) toe. 4, *E. dilatata f. lucksiana* (Hauer); (a) cross-section; (b) dorsal; (c) ventral; (d) trophi, apical; (e) swimming; (f-g, k) cross-sections; (h, j) different lorica forms; (i) *E. dilatata*, lateral, swimming. 5, *E. dilatata larga* Kutikova; (a) dorsal; (b) toe. Fig: 1:a-c, 2, 3a-c, 5a, b, after Kutikova (1970); 4a-d, j, k, after Hauer (1930); 4e-i, after Myers (1930). Scale lines 100 μ m.

Fig. 4: 1, *Euchlanis alata* Voronkov: (a) without wings, ventral; (b) with wings, ventral; (c) toe; (d) ventral; (e) habit, lateral; (f) cross-section. 2, *E. calpidia* (Myers); (a) dorsal, swimming; (b) trophi, apical; (c-f) cross-sections; (g) lorica, ventral. 3, *E. deflexa* Gosse; (a) dorsal; (b) lorica, ventral; (c, g, j), cross-sections; (d) trophi, apical; (e) toe, lateral; (f) other trophi; (h) dorsal; (i) resting egg; (k) lorica, broad form, ventral; (l) toe. 4, *E. deflexa larga* (Kutikova); (a) lorica, ventral; (b) toe. Fig. 4:a, d-f, after Yamamoto (1953); 1b, c, 3j, l, 4a, b, after Kutikova (1970); 2, 3a-e after Myers (1930); 3f-h, after Donner (1964). Scales lines 100 μ m (adults lorica in each number group).

μm , toes 34–240 μm . [*E. parva* Rousselet, 1892; dorsal plate length 140 μm , width 100 μm , ventral plate length 125 μm , width 75 μm , toes 70 μm , depth of posterior notch 50 μm].

Distribution: Cosmopolitan in fresh and brackish water; pH 4–10, Cl 140 mg l^{-1} (Koste 1978). The most common and widely tolerant euchlanid in inland waters; pancontinental, including Tasmania, 8.0–29.9°C, pH 5.44–7.9, DO 3.6–13.8 mg l^{-1} , 23–1600 $\mu\text{s cm}^{-1}$, 2–235 NTU.

Literature: Myers 1930; Hauer 1935; Kutikova 1970; Ridder 1972; Koste 1978; Shiel & Koste 1979; Koste & Shiel 1980.

Euchlanis incisa Carlin

FIG. 6:1

Euchlanis incisa Carlin, 1939, p. 17.

Euchlanis iriqueira Hudson & Gosse, 1889, Pl. 23, Fig. 4.

Diagnosis: Body ovoid in shape, truncate in front with variable anterior notch; dorsal plate triradiate in cross-section with median keel extending from neck to angle of posterior v-shaped notch. Ventral plate completely developed. Longitudinal deep sulci connect both plates; foot two-jointed, setae on first foot joint; toes slender, fusiform; trophi (Fig. 6:6e, b) with five teeth on each uncus. First and last (Fig. 6:11) have accessory shorter tooth; minute combs on rami tips. Male (Fig. 6:11) with normal anatomy for genus (cf. Fig. 3:1).

Length of dorsal plate 210–270 μm , ventral plate 180–240 μm , lorica width to 240 μm , toes 70–85 μm ; male 145 μm , toes 26 μm .

Distribution: Cosmopolitan in the littoral, occasionally in the pelagic of shallow ponds and billabongs. Rare, N.T., Tas., Vic: 13.5–29.9°C, pH 5.3–7.9, DO 5.45–8.2 mg l^{-1} , 23.0–80.2 $\mu\text{s cm}^{-1}$, 2.0 NTU.

Comment: A variant, *E. trifasciata mucronata* (= *E. incisa mucronata*) (Fig. 6:2a, b) described by Ahlstrom (1934) from the Neotropics may be an ecotype; it resembles *E. incisa* and may co-occur. The dorsal plate has an elongated keel. Length of dorsal plate to 320 μm , lorica width to 252 μm , height to 120 μm ; toes to 120 μm . Not yet recorded from Australia.

Literature: Myers 1930; Wulfert 1956; Koste 1974, 1978, 1981; Shiel & Koste 1979; Berzins 1982.

Euchlanis lyra Hudson

FIG. 6:3a–j

Euchlanis lyra Hudson In Hudson & Gosse, 1886, p. 89, Fig. 23:1

E. myersi Kutikova, 1959, p. 223.

Diagnosis: Body elongate and ovoid; cross-section resembles arc of circle; lateral sulci present; dorsal plate without posterior notch; ventral plate totally

developed, somewhat constricted caudally; foot slender, two-jointed; paired long setae on first foot joint; trophi with five paired unequal teeth, with two or three accessories; rami tips with minute inside comb. Length of toes variable.

Length of dorsal plate to 335 μm , ventral plate 302 μm , lorica width 110–180 μm , toes 76–90 μm , toe width 14–16 μm .

Distribution: Cosmopolitan in inundation areas, also in periphyton. Single record from L. Mulwala, Vic: 12.0°C, pH 7.5, DO 10.7 mg l^{-1} , 46 $\mu\text{s cm}^{-1}$, 17.5 NTU. Variants are known in the northern hemisphere; e.g. *E. lyra myersi* (Kutikova 1959: 223) (Fig. 6:4) a Palearctic subspecies with long slender toes (86–107 μm long, 7–8 μm wide) and *E. lyra larga* (Fig. 6:3k, l) (Kutikova 1959) from N. Siberia. Variants are not recorded from Australia.

Literature: Myers 1930; Pejler 1962; Koste 1978; Shiel & Koste 1979.

Euchlanis meneta Myers

FIGS 7:1,2

Euchlanis meneta Myers, 1930, p. 378, Pl. 19, Figs 5–8.

Euchlanis orophila Lucks, 1912, p. 105, Fig. 31.

Euchlanis proxima Myers, 1930, p. 377, Pl. 19, Figs 1–4.

Diagnosis: Shape nearly ovoid; well-developed ventral plate almost as large as dorsal plate; cross-section semicircular arched but also roughly triradiate; dorso-ventral width of lateral sulci (relatively) uniformly wider than in any other congener; cuticular shield-like process beneath posterior notch above first foot joint; posterior notch of dorsal plate very deep and often large (Fig. 7:1k); foot two-jointed; toes very long and slender, sometimes with minute claw at tips. Male colourless, with short toes; dorsal and ventral plate still conspicuous; brain long with red eye; two sensory hairs on tiny tubules in apical field, as in female. Trophi (Fig. 7:1e) with four main teeth, accessories not visible; minute denticulate combs on inside of rami tips (Figs 7:1e, 2d).

Length of dorsal plate 105–173 μm , width 80–140 μm , depth of posterior notch 35–45 μm , width of ventral plate 50–90 μm , toes 60–75 μm , width of toes 3.5 μm . Male total length 170 μm , toes 25 μm . **Distribution:** Cosmopolitan, mostly in acidic waters; rare in submerged *Sphagnum*; N. America, W. Germany, N.S.W., N.T., Vic., W.A. 10.0–29.9°C, pH 5.3–7.4, DO 5.45–10.1 mg l^{-1} , 20–523 $\mu\text{s cm}^{-1}$, 22 NTU, alk. 2.6–2.7 mg l^{-1} .

Literature: Myers 1930; Hauer 1935 (*proxima*); Wulfert 1951; Pejler 1962; Berzins 1963, 1982; Koste 1978, 1981; Koste & Shiel 1980.

Euchlanis orophila Gosse

FIG. 8:1

Euchlanis orophila Gosse, 1887, p. 5, Fig. 2:16,

nom. *Euchlanis orophila* Lucks, 1912, p. 105, Fig. 31.

Diagnosis: Resembles *E. dilatata* but usually smaller, with stouter foot and more robust, differently-shaped fusiform toes; lateral antennae situated in cavities beside somewhat keeled end of dorsal plate; trophi construction as *E. dilatata* (cf. Figs 3e, 5:4d). Comb-like processes on inside of each ramus tip; four opposed club-shaped functional teeth.

Length of dorsal plate 164–266 µm, width 127–172 µm, ventral plate length 123–225 µm, toes 49–78 µm, width 10–14 µm, posterior notch 25–29

Distribution: Cosmopolitan. N.T., Qld., Vic. 8.0–18.5°C, pH 4.8–8.4, DO 8.4–10.0 mg l⁻¹, 67–400 µS cm⁻¹, 4.5–160 NTU.

Literature: Myers 1930; Kutikova 1959; Koste 1978; Shiel & Koste 1979; Berzins 1982.

Euchlanis parmeneta Berzins

FIG. 7:3

Euchlanis parmeneta Berzins, 1973, p. 126, Figs. 4, 5.

Diagnosis: Resembles *E. meneta* (see above). Toes with pseudoclaws; anterior margin of dorsal plate with two short keels.

Length of dorsal lorica 95–104 µm; ventral plate 70–72 µm; width, dorsal 70–75 µm, ventral 50–55 µm; anterior margin width 35 µm, caudal opening 26–30 µm long x 18–25 µm wide; toes 45–50 µm.

Distribution: Recorded from New Zealand, not yet known from Australia.

Euchlanis phryne Myers

FIG. 8:2

Euchlanis phryne Myers, 1930, p. 372, Pl. 14, Fig. 1: Pl. 15, Figs 1–4.

Diagnosis: Dorsal lorica oval, with slight constriction of median lateral margin; deep inverted U-shaped caudal notch almost as long as toes; stiffened ventral plate connected to dorsal plate by longitudinal sulci; toes short, fusiform, ca. ¼ length of dorsal plate; trophi with four club-shaped teeth on each ramus; rami with fan-shaped denticulate combs on inner distal margins.

A superficial resemblance to *E. pyriformis* and *E. calpidia* was noted by Myers (1930), and Koste (1978) considered *E. phryne* a possible variant of *E. calpidia* or *E. dilatata*. Comparison of lorica morphology of the species above, particularly cross-sections, and differences in trophi structure, indicates that *E. phryne* is a distinct species.

Length of dorsal plate 225 µm, ventral plate 210 µm, dorsal width 180 µm, ventral plate width 150 µm, toes 65 µm.

Distribution: North America (Maine); single locality, a billabong of the Goulburn R. near Seymour, Vic., in spring 1976 and again in summer 1978. 17.0–22.0°C, pH 7.1–7.4, DO 8.7–9.8 mg l⁻¹.

Comment: The above anomalous distribution is noteworthy: *E. phryne* is one of several rotifer and microcrustacean species recorded from Goulburn River billabongs with similar disjunct distributions (Shiel 1976 and unpublished data; Koste 1979). The importation of heavy dam-building machinery by the Utah Construction Company in the mid-1950's (during the construction of Eildon Dam) is implicated as a possible source of transport of resting eggs/ephippia. Populations have become established in sheltered billabongs downstream of the dam site.

Euchlanis pyriformis Gosse

FIG. 8:3

Euchlanis pyriformis Gosse, 1851, p. 201.

Dapidia pyriformis Myers, 1930, p. 370, Fig. 15:5–7.

Diagnosis: Shape nearly circular, may have slight emarginations instead of caudal notch; lateral margins turned downwards, occasionally pinched in the middle; ventral plate rudimentary, only developed posteriorly; no lateral sulci; foot two-jointed; two long pairs of setae on dorsal side of the first foot segment; toes relatively short; trophi resembles that of *E. deflexa* (cf. Fig. 4:3f).

Length of dorsal plate 285–320 µm, width 275–315 µm, toes 80–85 µm, toe width 10–13 µm.

Distribution: Cosmopolitan in the littoral, occasionally pelagic. Vic., Tas.

Literature: Koste 1978; Berzins 1982; Shiel & Koste 1985.

Euchlanis triquetra Ehrenberg

FIG. 9:1

Euchlanis triquetra Ehrenberg, 1838, p. 461, Fig. 57:8.

E. pellucida Herring, 1921, p. 6, Fig. 2.

E. langobardica Mansfeld, 1927, p. 24, Fig. 7h.

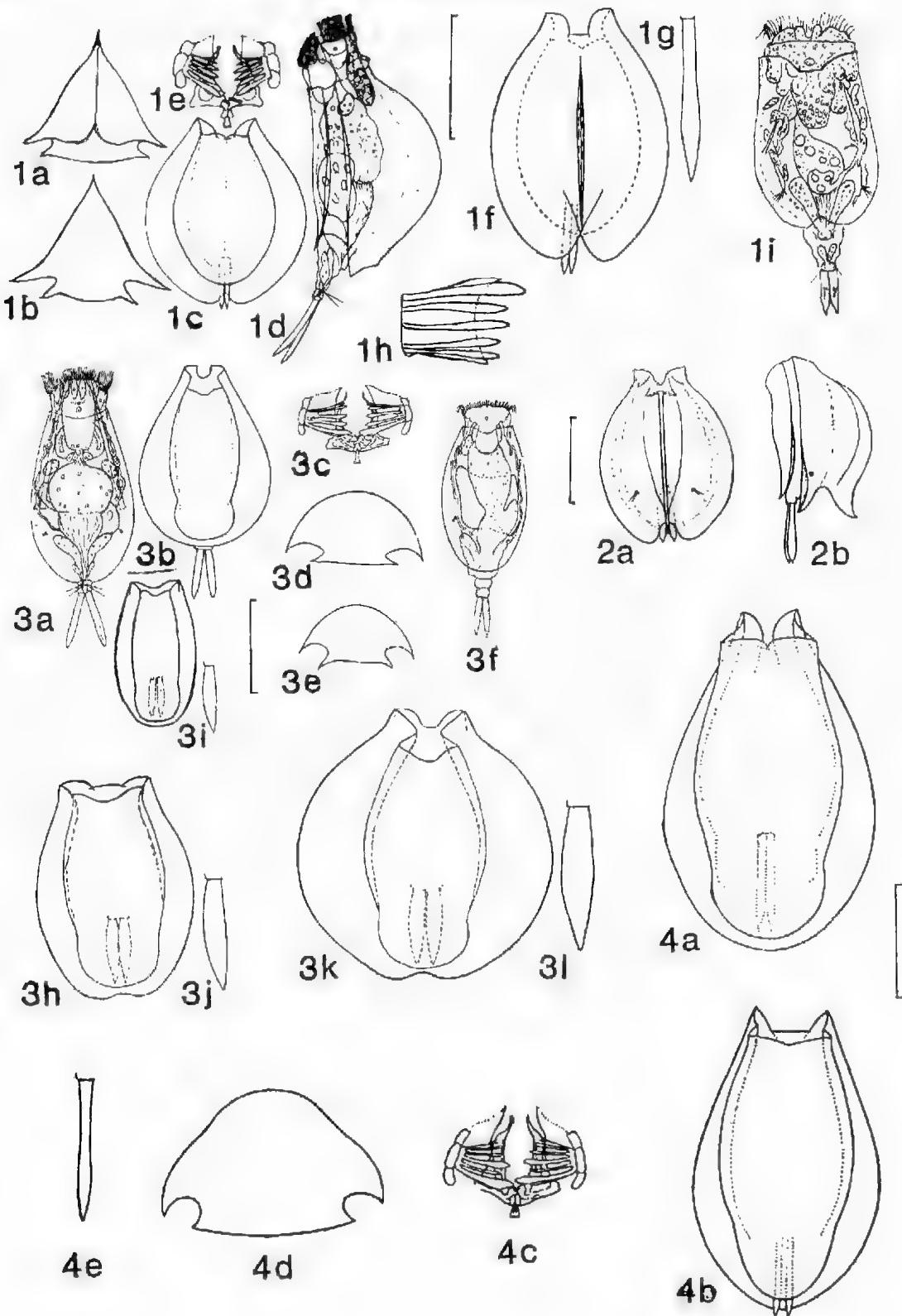
Dapidia carinata Carlén-Nilsson, 1934, p. 6, Fig. 2.

D. lata Carlén, 1939, p. 16.

Euchlanis triquetra pterigoides Crete, 1955, p. 60, Figs 15, 19.

non-*E. triquetra* after Ruttner-Kolisko, 1972, p. 182, Fig. 11b.

Diagnosis: Body in dorsal view circular, sometimes somewhat elongated (Fig. 9:1); triangular with a high keel in cross-section; median keel extends from neck to caudal region; dorsal plate laterally with wide flanges (Fig. 9:1c–e); no ventral plate, no posterior notch, no lateral longitudinal sulci; some specimens with semicircular ventral line over base of toes; foot obscurely two-jointed; toes long, slender, nearly straight, ending in abrupt points; most loricas very transparent with coloured inner organs (retrocerebral sac dark, mastax yellow, stomach olive green, yellow or brownish). Male (Fig. 9:3l,i) with cuticular plates and dorsal keel. Trophi cf. Fig. 9:1j–n; tips of rami with minute combs (Fig. 9:1j–k).



Lorica length 300–710 µm, width to 540 µm, toes 90–15 µm, lorica height to 300 µm, trophi: ram 40 µm, fulcrum 32 µm, manubria 50 µm.

Distribution: Cosmopolitan in the littoral, sometimes pelagic in shallow waters, N.S.W., Qld., N.T., Vic.

Literature: Peijer 1962; Koste 1978, 1981; Shiel & Koste 1979; Berzins 1982.

The following species are not considered here:

E. urenosa Myers, 1936, known only from N. America and ?Volga;

E. biciliata Issei, 1901 (*nomen nudum*; name published without description, and apparently later synonymized with *E. plicata* Levander by Issei (1906). Incorrectly cited in Voigt (1957) and Koste (1978);

E. callysta Myers, 1930 (Fig. 9:4) is possibly a juvenile form of *E. triquetra*. Only known from the Nearctic. Length of dorsal plate 170 µm, lorica width 80 µm, toes 50 µm. (Myers, 1930; Koste, 1978);

E. callinorpha Berzins, 1957 (Fig. 9:2) resembles *E. incisa*, only known from Gambia, W. Africa;

E. contorta Wulteri, 1939, known only from central Germany and the Volga estuary;

E. dipadiata Parise, 1966, see Koste 1978 (misquoted as Parise, 1963). Doubtful species;

E. hyphidactyla Parise, 1963, see Koste 1978. Doubtful species.

E. ligulata Kutikova & Vasmileva, 1982, endemic in Lake Baikal;

E. mamorokuensis Berzins, 1973 (Fig. 9:3), recorded from Madagascar;

E. mikropous, Koch-Althaus, 1962; recorded only from central Germany;

E. pannonica Barisch, 1871, known only from Hungary, single record;

E. perpusilla Ridder, 1977, known only from the Caribbean;

E. turfusa (Rodewald, 1940), known only from Romania.

Family Mytilinidae Bartos

Loricate rotifers; cross-sections of lorica mostly triangular or nearly rhombic; ventral plate and dorso-lateral plates firmly fused; long dorsum with or without sulcus, latter common with double keel; three or less foot sections; toes pointed, straight or slightly curved ventrally; malleate trophi. All species littoral and benthic, occasionally (but rarely) in the plankton. Two genera (see Bartos 1959, Kutikova 1970, Koste 1978).

Key to genera of Mytilinidae

1. Lorica thin or rigid with dorsal sulcus and double keel; lorica unornamented; toes long

..... *Mytilina* Bory de St Vincent
Lorica without dorsal sulcus, one strong keel; lorica

ornamented with distinct pattern and cavities; toes short

Lophocharis Ehrenberg

Genus *Mytilina* Bory de St Vincent

Mytilina Bory de St Vincent, 1826, p. 87. (= *Salpina* Ehrenberg, 1830, p. 46 = *Diplax* Gosse, 1851, p. 201 = *Diplacidium* Lauterborn, 1913, p. 483).

Two recognized form-series ("Formenkreise"). One series strongly loricate, usually with variable stiff anterior and posterior spines; anterior margin of lorica generally granulated; toes stiff and sword-shaped. Second group thinly loricate without anterior spines (except *M. acanthophora*, (Fig. 10:1, 2); anterior margin not granulate, toes mostly long and slightly curved, flexible.

Key to Species of the Genus *Mytilina*

1. Lorica stout, anterior margin granulated, toes sword-shaped..... 2
2. Lorica thin, anterior margin not granulated, toes long and curved..... 3
- 2(1). Anterior lorica margin with two short dorsal and two short ventral spines. *M. mucronata* Müller
Anterior lorica margin with only two ventral spines..... *M. ventralis* (Ehrenberg)
- 3(1). Ventral margin of lorica with variable projections..... *M. acanthophora* Hauer
Ventral-anterior margin without projections..... 4
- 4(3). Toes with claws..... 5
- 4(3). Toes without claws..... 6
- 5(4). Head part loricate; 3 foot segments..... *M. crassipes* (Lucks)
Head part illoricate; 2 foot segments..... *M. unguipes* (Lucks)
- 6(4). Toes relatively short; anterior margin of lorica with folds..... *M. hispilata* Lucks
Toes long, straight, anterior margin without folds (sembles *M. acanthophora*). *M. trigona* (Gosse)

Mytilina acanthophora Hauer

FIGS 10:1,2

Mytilina acanthophora Hauer, 1938, p. 550, Figs 73a-c.
Diagnosis: Dorsal lorica strongly arched, granulated; ventral lorica flattened, with depression beneath head opening; triangular lorica projections flank medioventral head aperture (Fig. 10:1b); shield-like projection over two-segmented foot; toes long, pointed.

Length: 135–253 µm (total); 10–150 µm (lorica); height to 92 µm; width to 64 µm; toes 90–94 µm. An unusually large specimen from Lago Grande, Amazonia had the following measurements (sequence as above): 342, 198, 125, 137, 140–144 µm (Koste unpubl.).

Distribution: Probably pantropical in polysaprobic waters. Not yet recorded from Africa. Occasionally

Fig. 6: 1, *Euchlanis incisa* Carlin: (a, b) lorica cross-sections; (c) ventral; (d) lateral, swimming; (e) trophi, apical; (f) dorsal; (g) toe; (h) uncus; (i) male. 2, *E. incisa mucronata* (Ahlsrom): (a) dorsal; (b) lateral. 3, *E. lyra* Hudson: (a) dorsal; (b) ventral; (c) trophi, apical; (d, e) cross-sections; (f) dorsal, swimming; (g, h) lorica, ventral; (i) toe; (j) trophi, apical; (k) *E. lyra larga* (Kutikova), ventral; (l) toe. 4, *E. lyra myersi* (Kutikova): (a) ventral; (b) another form, ventral; (c) trophi, apical; (d) cross-section; (e) toe. Fig. 6: 1a–e, 3a, b, 4a–d, Myers (1930); 1f, g, 3c–l, 4c, after Kutikova (1970); 2a, b, after Koste (1974). Scales lines 100 µm (adult lorica in each number group).

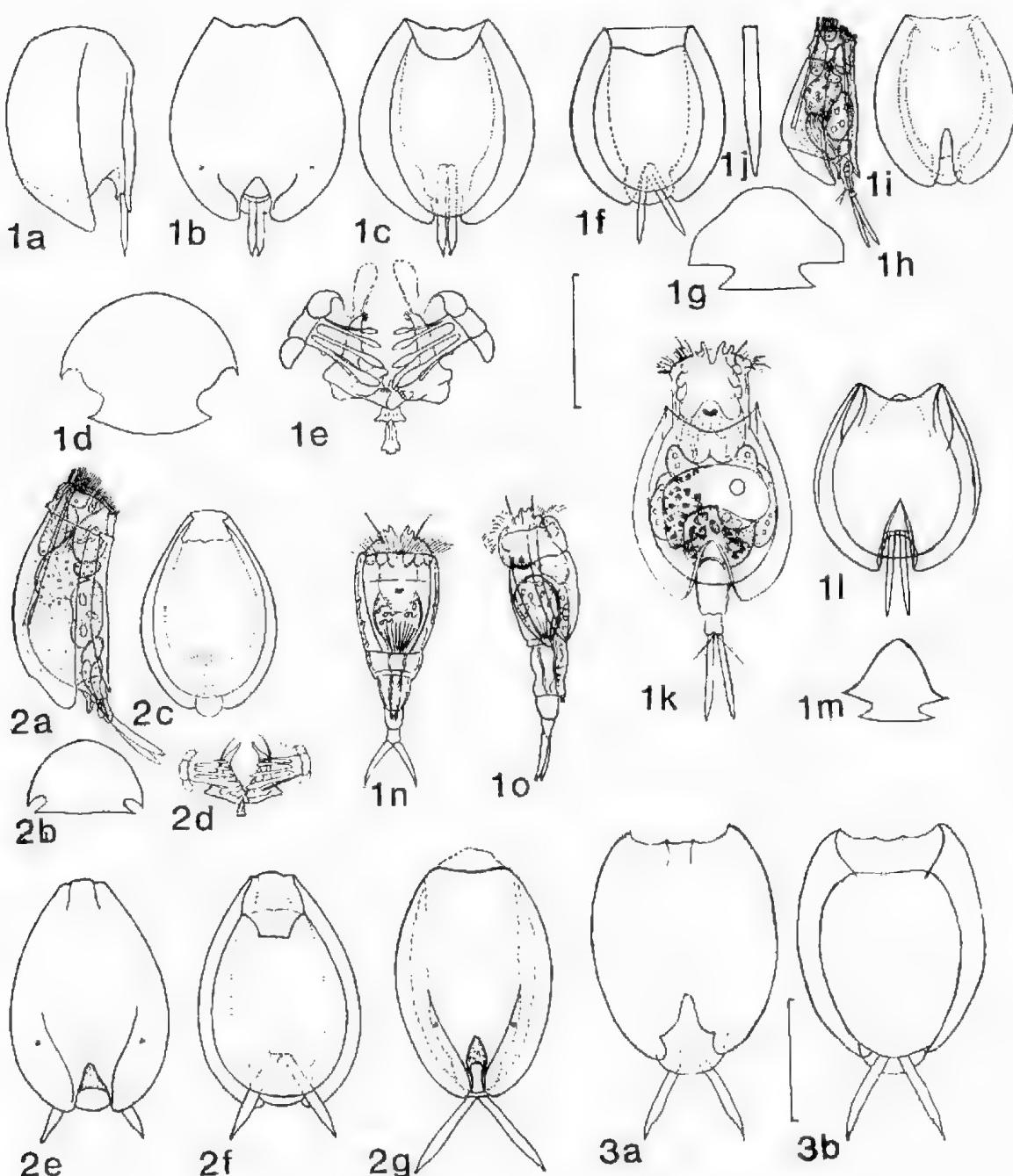


Fig. 7: 1, *Euchlanis meneta* Myers: (a) lateral; (b) dorsal; (c) ventral; (d) lorica cross-section; (e) trophi apical; (f) lorica ventral; (g) cross-section; (h) lateral, swimming; (i) lorica dorsal; (j) toe; (k) dorsal, swimming; (l) dorsal; (m) cross-section; (n) male; (o) male, lateral. 2, *E. proxima* Myers: (a) lateral, swimming; (b) cross-section; (c) ventral; (d) trophi, apical; (e) dorsal; (f) ventral; (g) dorsal. 3, *E. parameneta* Berzins: (a) dorsal; (b) ventral. Fig. 7:1a-e, 2e-g, after Hauer (1935); 1f, g, i, j, after Kutikova (1970); 1k, o, after Wulfert (1960); 3a, b, after Berzins (1973); 2a-d after Myers (1930). Scale lines, top, 100 µm (Fig. 7:1, 2), bottom, 50 µm (3a, b).

in plankton samples. Qld (Townsville, Mt Isa).
Literature: Koste 1978; Shiel & Koste 1985.

Mytilina bisulcata (Lucks)

FIG. 10:3

Diplax bisulcata Lucks, 1912 p. 95, Figs. 28a-c.
M. trigona after Herring, 1913 p. 75.

Diagnosis: Lorica with folds on anterior margin; three weak dorsal keels in cross-section; sulcus indistinct; toes shorter than in *M. unguipes* with long tips (cf. *M. unguipes* (Fig. 12:2)).

Length 130–180 µm, toes 60–70 µm, tips 8–14 µm.
Distribution: In peat bogs, areas of decomposition. N.T., Vic.

Literature: Hauer 1936; Koste 1978; Koste & Shiel 1980; Berzins 1982; Tait et al. 1984.

Mytilina crassipes (Lucks)

FIG. 10:4

Diplax crassipes Lucks, 1912, p. 96, Fig. 30.
Mytilina crassipes after Carlin-Nilsson, 1934, p. 11.

Diagnosis: Lorica laterally compressed; head with two lateral rounded plates; trophi small, uncus with six teeth; mouth opening with palpal organs; stomach and gastric glands large; two black spots at "forehead" region (?eyes).

Length 220–280 µm (total); lorica 138 µm; toes 57–75 µm; claw 9 µm; trophi 21–30 µm.

Distribution: Cosmopolitan in polysaprobic waters, occasionally in shallow-water plankton. N.T. (Magela Ck.).

Literature: Koste 1978, 1981; Koste & Shiel 1980; Tait et al. 1984.

Mytilina mucronata (Müller)

FIG. 11:1

Brachionus mucronatus Müller, 1773, p. 134.
Mytilina mucronata after Hofsten, 1909, p. 54.
 See Koste (1978) for extensive synonymy.

Diagnosis: Shape of lorica variable, of little taxonomic value (e.g. *M. mucronata* var. *spinigera* (Ehrenberg, 1832)); corona as in *Euchlanis*; lorica granulated anteriorly; dorsally curved spines visible in lateral view beside foot opening; keels end in short hook; foot three-segmented; large cerebral eye present (Fig. 11:1a eye lateral antennae indistinct; dorsal antenna (Fig. 11:1a da) visible; trophi of malleate type, uncus with five teeth; mastax (Fig. 11:1a mv) with salivary glands; stomach cellular with small gastric glands (Fig. 11:1a gg). Male approximately half female size, also loricate with cerebral eye (cf. (Fig. 3:1, n)).

Length: 170–250 µm, height: 96–100 µm, toes 53–60 µm, subitanous egg 80 µm, male to 135 µm.
Distribution: Cosmopolitan in eutrophic waters; also on the surface of decomposition areas between water plants and in brackish waters. Occasionally in the plankton of shallow ponds and billabongs.

Vic. 13.5–22.0°C., pH 7.1–7.4, DO 4.1–10.2 mg l⁻¹, 240 µS cm⁻¹, 5 NTU.

Literature: Evans 1951; Koste 1978.

Mytilina trigona (Gosse)

FIG. 12:1

Diplax trigona Gosse, 1851, p. 201.
Mytilina trixona after Herring, 1913, p. 75.

Diagnosis: Surface of lorica slightly dotted; anterior margin with rounded edge ventrally (cf. *M. acanthophora* Fig. 10:1, 2); cross section almost triangular; narrow double keel; toes with long tips.

Total length: 245–265 µm, lorica length 150–160 µm, toes 68–83 µm.

Distribution: Cosmopolitan in decomposition/inundation areas, Qld.

Literature: Koste 1978; Shiel & Koste 1979; Berzins 1982.

Mytilina unguipes (Lucks)

FIG. 12:2

Diplax unguipes Lucks, 1912 p. 96.

Mytilina bisulcata f. *unguipes* (Lucks) after Carlin-Nilsson, 1934, p. 11.

Mytilina unguipes (Lucks) after Wiszniewski, 1953, p. 387.

Diagnosis: Anterior margin of lorica without folds, laterally compressed; foot with two joints; toes long, slightly curved with distinct, inflexible claw. Doubtful species, possibly identical with *M. bisulcata*.

Length 193 µm, height 94 µm, toes 58 µm, claw 13 µm.

Distribution: European peat bog, not yet recorded from Australia.

Literature: Kutikova 1970; Koste 1978

Mytilina ventralis (Ehrenberg)

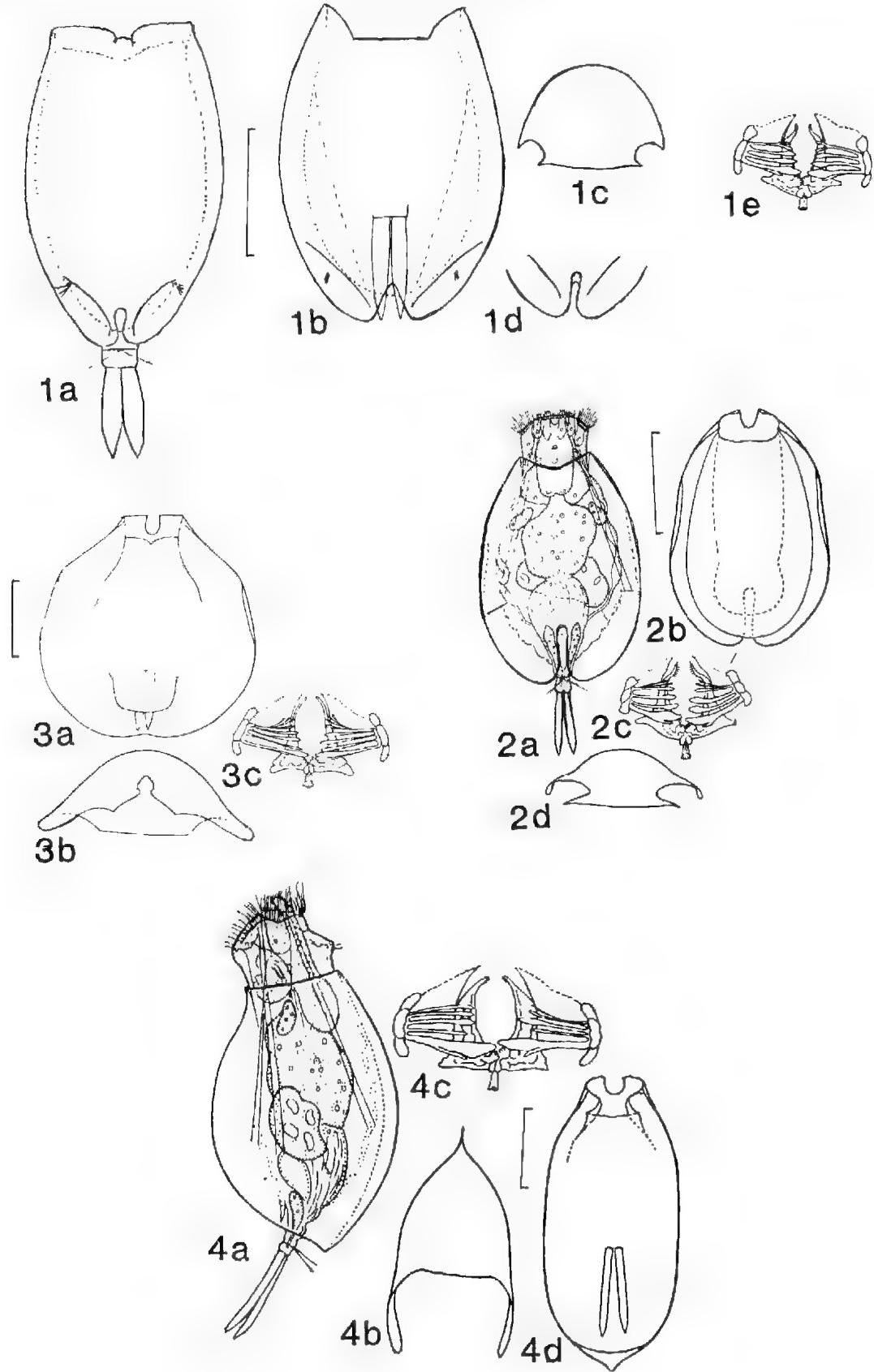
FIGS 11:3, 4, 5

Salpinta ventralis Ehrenberg, 1832, p. 133, PL 4, Fig. 7.
Mytilina ventralis (Ehrenberg) after Herring, 1913, p. 75.

For extensive synonymy see Herring (*loc. cit.*) and Kutikova (1970:519–520).

Diagnosis: Lorica margin granulated; shape and size of lorica and spines very variable; only ventral anterior spines. Short-spined form (var. *brevispina*, 176–215 µm) shown in Fig. 11:3a-c; long-spined form (var. *macracantha*, 250–350 µm) shown in Fig. 11:4. Fig. 11:5 shows rare form described by Wulfert (1965) (*M. ventralis* f. *longidactyla*) with short anterior but long median and shorter caudal ventral hooks. Lorica (90–115 µm) without spines, median caudal spine 62 µm, ventral caudal spines 48 µm, toes 72 µm. These forms may be ecotypes.

Distribution: Cosmopolitan. Probably pancontinental, not yet recorded from S. Aust. (f. typ. from N.S.W., N.T., Qld, Tas., Vic.; *brevispina* from N.T., Qld, Vic.; *macracantha* from N.T., Qld).



W.A. 13.5–28.5°C, pH 5.44–7.9, DO 5.8–10.6 mg l⁻¹, 23–1500 µS cm⁻¹, 6.8–67 NTU, alkalinity 2.7 mg l⁻¹.

Not yet recorded from Australia:

- M. incarnata* (Perty, 1850)
 - M. mucronata* (Jennings, 1894)
 - M. mutica* (Perty, 1849)
 - M. videns* (Levander, 1894)
- (see Koste 1978 for details).

Genus *Lophocharis* Ehrenberg

Lophocharis Ehrenberg 1838, p. 458.

Strong lorica, surface soft, granulated, but may have honeycomb structure; cross section nearly rhomboid but specimens with flexible integument nearly oval or compressed; dorsum always arched; more or less distinct keel with and without transverse folds; ventral plate with longitudinal and transverse ribs; apical margin with and without serration; ventral aperture rounded, dorsal more triangular; foot-opening ventral; foot with three joints; toes with sharp points; trophi malleate (Fig. 13:1d); cerebral eyes only visible in living animals. Littoral and benthic in habit, seldom found in the plankton. Seven species are known, four have been recorded from Australia.

Key to Species of the Genus *Lophocharis*

- 1. Lorica >120 µm long with distinct dorsal keel producing triangular cross-section 2
- 2. Lorica <100 µm long, keel indistinct, cross-section more elliptical, *L. curvata* Berzins
- 2(1). Anterior margin of lorica strongly serrated, dorsal keel with transverse folds *L. salpina* (Ehrenberg)
- 2(2). Anterior margin smooth or lightly serrated, dorsal keel without folds 3
- 3(1). Lorica smooth, dorsal notch of head aperture V-shaped, ventral a broader U-shape; fine striae on both sides of dorsal keel; *L. naias* Wulfert
- 3(2). Lorica sculptured as *L. salpina*; head aperture notches V-shaped; no striae beside keel *L. oxysternon* (Gosse)

Lophocharis curvata Berzins

FIG. 13:3

Lophocharis curvata Berzins, 1982, p. 12, Fig. 15a–c.
Diagnosis: Small species, lorica elongated U-shape without typical dorsal keel, cross section more dorso-ventrally flattened than in congeners; head aperture margin with dorsal and ventral sinuses; ventral slightly broader; foot aperture broadest posteriorly; toes thin, curved outwards.

Lorica length 95 µm, width 55 µm, toes 18 µm, foot aperture width 32 µm.

Distribution: Endemic; single record from King Parrot Ck, Kinglake, Vic. 18.x.53.

Comment: Although the original description and figures of this rotifer do not meet the requirements of the Code, we feel that the distinctive dorsum, foot-aperture and small size warrant retention of specific status until material can be examined.

Lophocharis naias Wulfert

FIG. 13:4

Lophocharis naias Wulfert, 1942, p. 188, Fig. 1a k.

Diagnosis: Dorsal lorica with shallow keel and lateral longitudinal striations, surface morphology otherwise smooth, unornamented; apical margin of lorica finely serrated; uncus with 7 teeth; inner margin of rami with fine denticles.

Lorica length to 170 µm, width to 105 µm; toes to 21 µm.

Distribution: Europe. Single record, from Coongie Lakes, S. Aust., coll. Jane Roberts, Botany Dept., Univ. of Adelaide, 06.xii.86.

Literature: Koste 1978.

Lophocharis oxysternon (Gosse)

FIG. 13:1

Metopidia oxysternon Gosse, 1851, p. 201.

Lophocharis oxysternon (Gosse) after Harring, 1916, p. 564, Fig. 97:6–13.

Diagnosis: Surface of integument soft or weakly pustulated; ventral plate with deep depression over foot-opening. Many intermediate forms to *L. salpina*, e.g. with slightly serrated apical margin. Trophi (Fig. 13:1d–e) with six uncus teeth.

Lorica length 120–200 µm, toes 24 µm.

Distribution: Cosmopolitan, benthic in fresh and brackish waters, occasionally in plankton. Vic.

Literature: Koste 1978, Berzins 1982.

Lophocharis salpina (Ehrenberg)

FIG. 13:2

Lepadella salpina Ehrenberg, 1834, p. 209.

Metopidia salpina after Hudson & Gosse, 1889, p. 46, Fig. 34:4.

Lophocharis salpina (Ehrenberg) after Harring, 1916, p. 563.

For extensive synonymy see Koste (1978:151).

Diagnosis: Anterior margin always serrated; keel with transverse folds mostly over caudal part of lorica; variable, intermediate forms to *L. oxysternon*; trophi also with six uncus teeth; foot with three joints; toes sharply pointed, ventrally curved.

Length 175–224 µm, loricae 120–135 µm; width

Fig 8: 1, *Euchlanis orophila* Gosse: (a) dorsal; (b) dorsal; (c) cross-section; (d) alternate caudal loricas; (e) trophi, apical. 2, *E. phryne* Myers: (a) dorsal; (b) ventral; (c) trophi, apical; (d) cross-section. 3, *E. pyriformis* Gosse: (a) ventral; (b) lorica cross-section; (c) trophi. 4, *E. callystoma* Myers: (a) lateral; (b) cross-section; (c) trophi; (d) ventral. Fig. 8:1a, after Koste (1978); 1–d, after Donner (1964); 1c, 2a–d, 3a–c, 4a–d, after Myers (1930). Scale lines 100 µm (Fig. 8:1–3); 50 µm (4a, b, d).

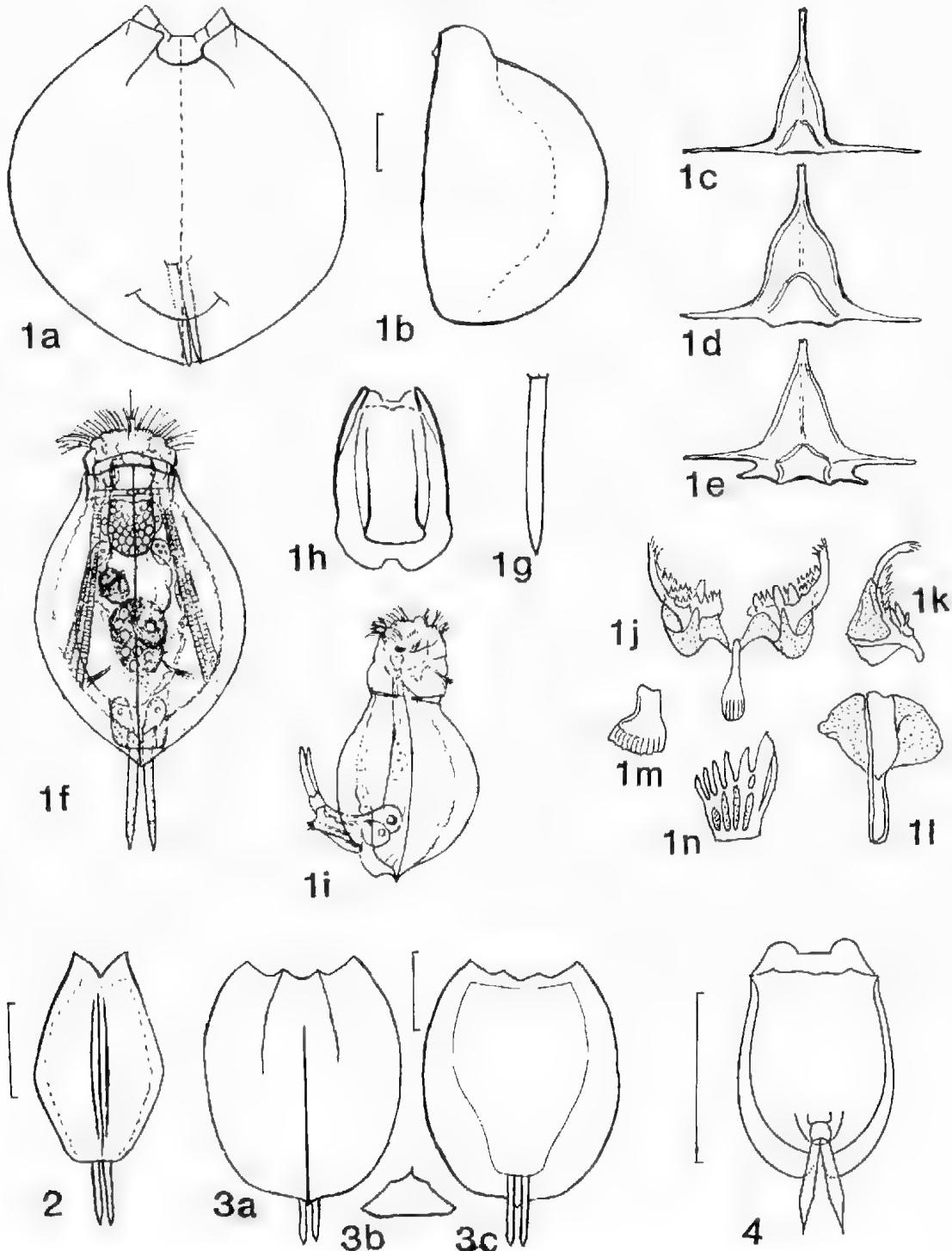


Fig. 9. 1, *Euchlanis triquetra* Ehrenberg, (a) lorica, ventral; (b) lateral; (c–e) different cross-sections; (f) dorsal, swimming; (g) toe; (h) male, contracted; (i) male, lateral, swimming; (j) trophi (fulcrum and rami); (k) ramus; (l) manubrium; (m) fulcrum; (n) uncus. 2, *E. callimorpha* Berzins, dorsal. 3, *E. mamorokaensis* Berzins; (a) dorsal; (b) cross-section; (c) ventral. 4, *E. perpusilla* Ridder, ventral. Fig. 9:1a, after Kutikova (1970); 1b–e, after Grese (1955); 1f–n, after Wulfert (1956); 2, 3a–c, after Berzins (1973); 4, after Ridder (1977). Scale lines 100 µm (adult lorica in each number group).

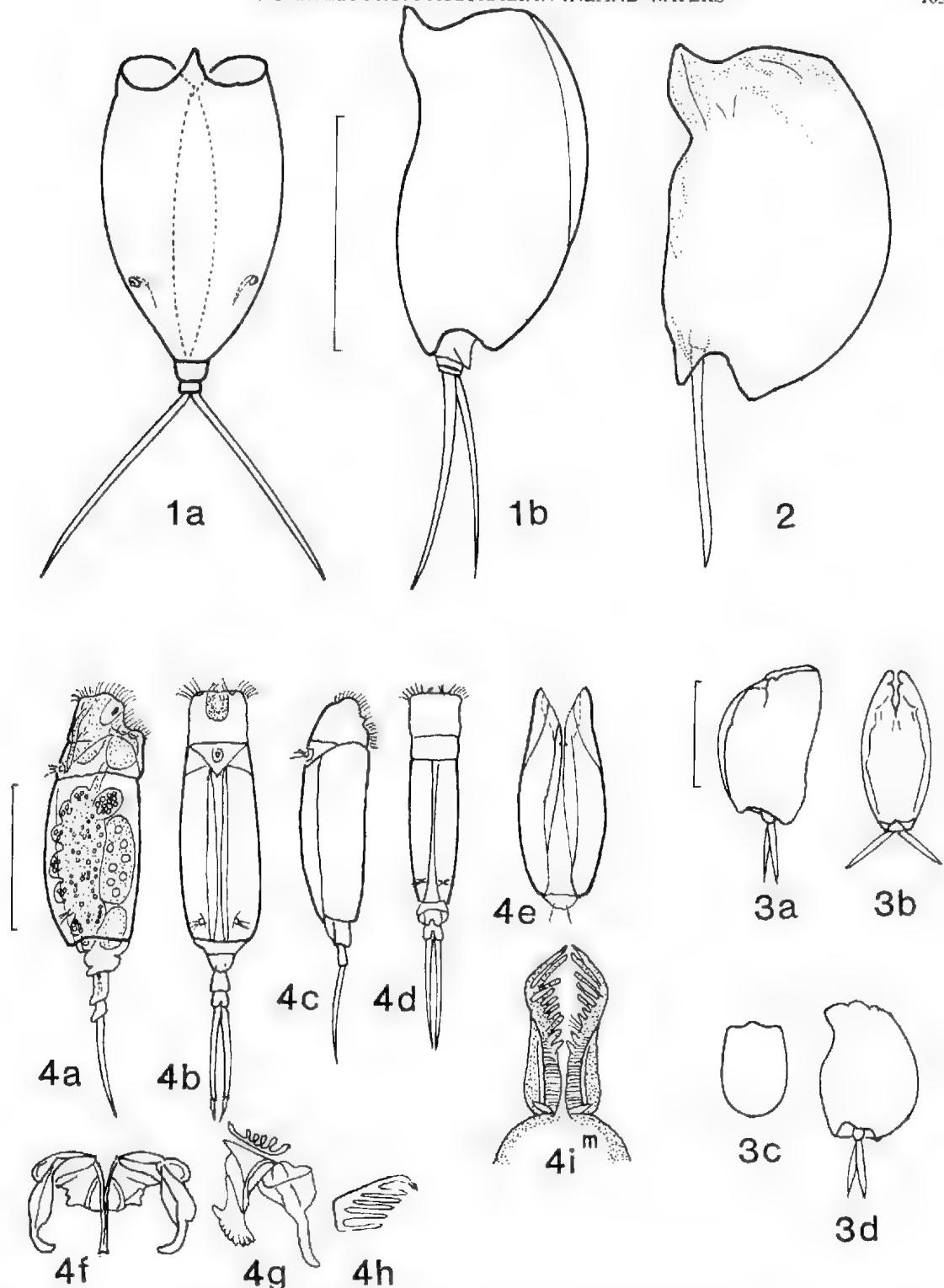


Fig. 10: 1, *Mytilina acanthophora* Hauer from Magela Ck, N.T.: (a) ventral; (b) lateral; (c) cross-section; (d) lateral (cf. 3a, b). 4, *M. crassipes* (Lucks): (a) lateral; (b) dorsal; (c) lateral; (d) dorsal; (e) lorica, contracted; (f) trophi; (g) trophi, lateral; (h) uncus; (i) mouth with palpal organs ($m = \text{mouth}$). Fig. 10:3, after Hauer (1936); 4, after Wulffert (1939). Scale lines 100 μm (adult lorica in each number group).

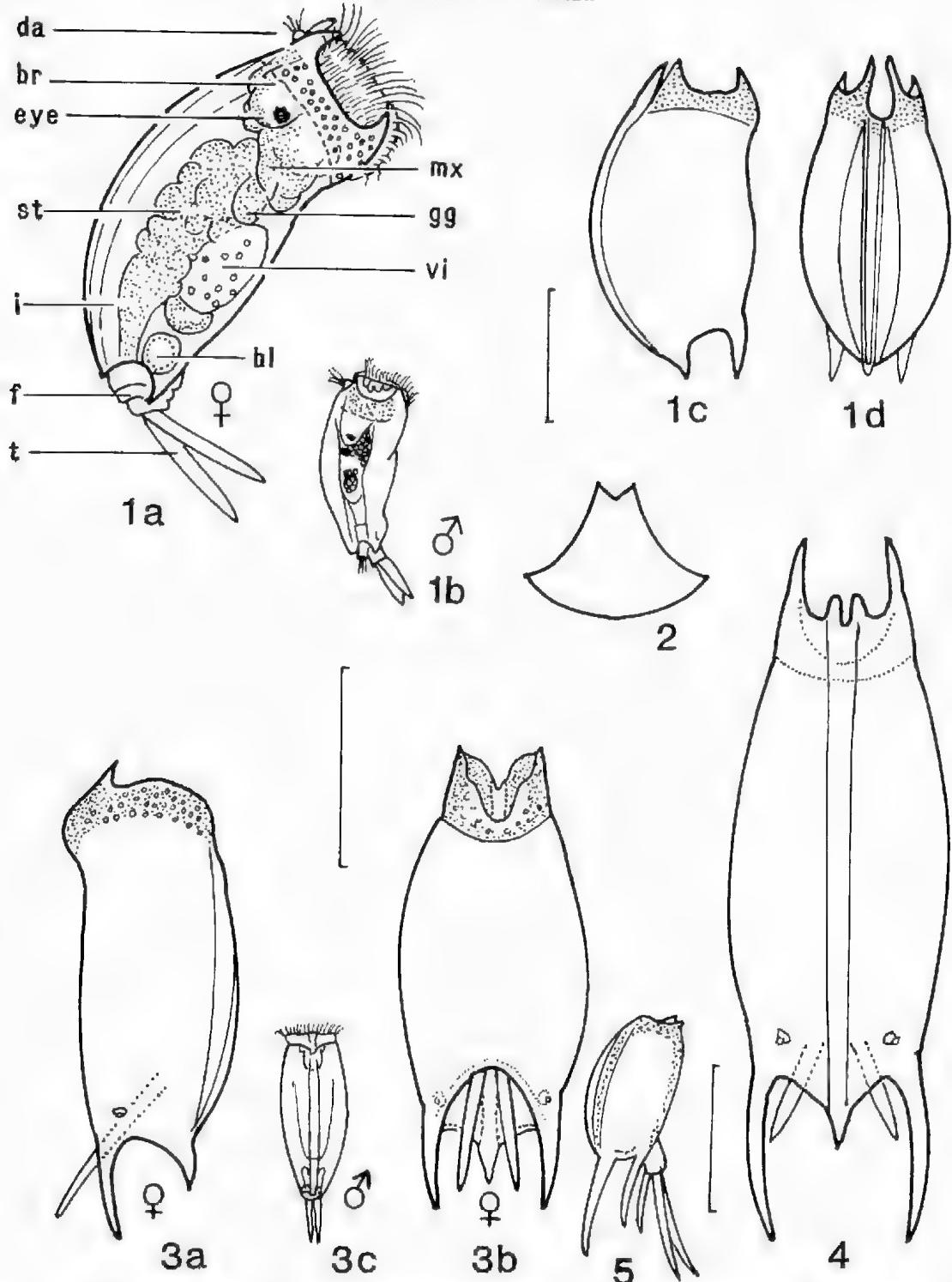


Fig. 11: 1, *Mytilina mucronata* (O. F. Müller): (a) swimming, lateral [*bl* = bladder, *br* = brain, *da* = dorsal antenna, *eye* = cerebral eye, *f* = foot, *gg* = gastric gland, *i* = intestine, *mx* = mastax, *st* = stomach, *t* = toe, *vi* = vitellarium]; (b) male, swimming, lateral; (c) lorica, lateral; (d) lorica, dorsal; 2, *Mytilina* sp. cross-section. 3, *M. ventralis* (Ehrenberg): (a) lorica, lateral; (b) ventral; (c) male, dorsal. 4, *M. ventralis macracantha* (Gosse) lorica, dorsal. 5, *M. ventralis longidactyla* (Wulffert), lateral, from E. Africa. Fig. 11:1a, 2, 3a, b, 4, after Koste (1978); 1b, c, after Pejler (1962); 1d, 3c, after Weber (1898); 5, after Wulffert (1965). Scale lines 100 µm. Top Fig. 11:1b-d; left, 3, 4; bottom, 5.

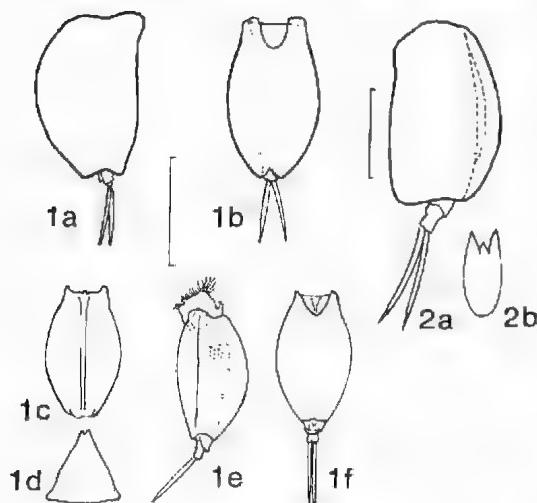


Fig. 12: 1, *Mytilina trigona* (Gosse); (a) lateral; (b) ventral; (c) lorica, dorsal; (d) cross-section; (e) swimming, lateral; (f) ventral. 2. *M. unguipes* (Lucks); (a) lateral; (b) cross-section. Fig. 12:1, after Donner (1954); 2, after Hauer (1936). Scale lines 100 μm .

80–95 μm , toes 25–40 μm .

Distribution: Cosmopolitan, benthic in fresh and brackish waters, also in polysaprobic pools and ponds. Pancontinental, 10.5–30.4°C, pH 5.6–8.4, DO 3.7–11.0 mg l⁻¹, 28–3330 $\mu\text{S cm}^{-1}$, 5–92 NTU, alkalinity 4.0 mg l⁻¹.

Literature: Evans 1951; Shiel & Koste 1979; Koste 1981; Berzins 1982.

Not yet recorded from Australia:

Lophocharis hutchinsoni Edmondson, 1935

L. naia f. ambidenta De Ridder, 1960

L. parva Rudescu, 1960

L. rubens Wulfert, 1939

(see Koste 1978 for details).

Family Trichotriidae Bartos 1959

Three genera with loricate head and body; surface with facets, mostly granulated and with spicules or spines, sec. on dorsum; foot freely movable or with stiff joints; trophi malleate. Generally occur between aquatic macrophytes and in periphyton. In plankton only as migrants.

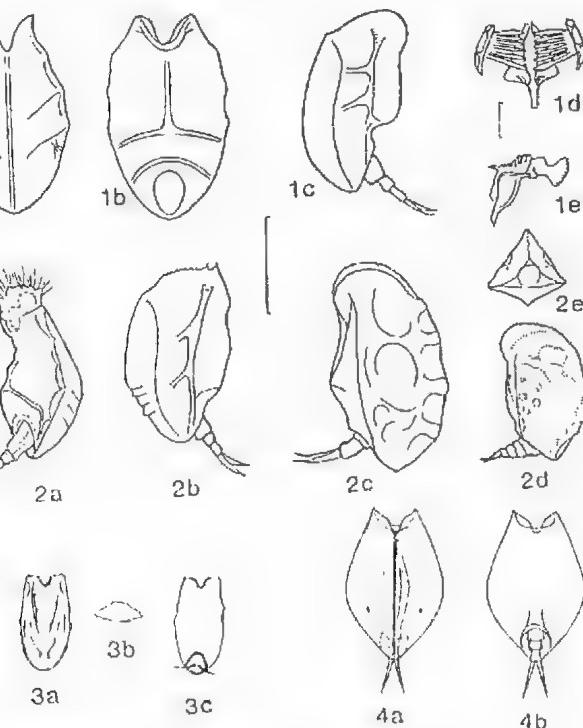


Fig. 13: 1, *Lophocharis oxysternon* (Gosse); (a) dorsal; (b) ventral; (c) lateral; (d) trophi, apical; (e) trophi, lateral. 2, *L. sulcina* (Ehrenberg), (a) swimming, lateral; (b) lorica, lateral; (c) lateral; (d) another lorica, lateral; (e) cross-section. 3, *L. curvata* Berzins, (a) lorica, dorsal; (b) cross section; (c) lorica, ventral. 4, *L. naia* Wulfert, (a) lorica, dorsal; (b) lorica ventral. Fig. 13:1 a–e, 2b, after Herring (1916); 2a, after Wulfert (1956); 1d, 2c, after Hauer (1925); 2d, after Clement (1960); 3 after Berzins (1982); Scale lines, centre, 100 μm (1a–c, 2–4); top right, 10 μm (d, e).

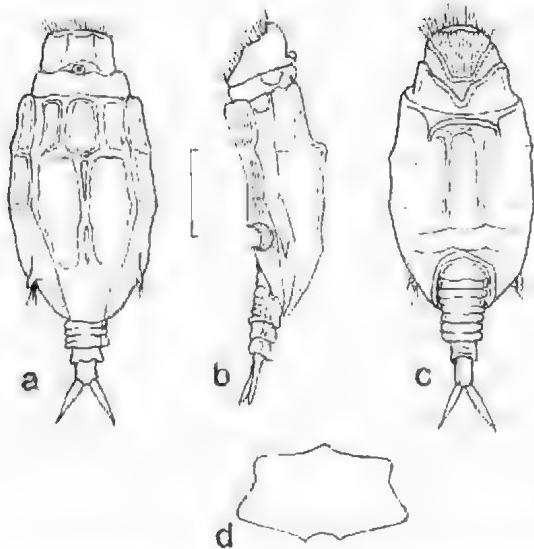


Fig. 14: *Wolga spinifera* (Western): (a) dorsal, swimming; (b) lateral; (c) ventral; (d) cross-section a-c, after Western (1894); d, after Vranovsky (1957). Scale line, 50 µm.

Key to genera of Trichotriidae

1. Lorica with anal segment..... 2
- Lorica without anal segment, ... *Wolga* Skorikov
- 2(1). Lorica with distinct elongated spines on dorsum
..... *Macrochaetus* Petty
No long spines on lorica
..... *Trichotria* Bory de St Vincent

Genus *Wolga* Skorikov

Wolga Skorikov, 1903, p. 37.

Monospecific, *Wolga spinifera*.

Wolga spinifera (Western)

FIG. 14

Distyla spinifera Western, 1894, p. 427, Fig. 2111-4.

Calyptina spinifera after Murray, 1913, p. 545-564.

Lecane spinifera after Herring, 1913, p. 62.

Wolga spinifera (Western) after Skorikov, 1903, p. 37.

Diagnosis: Dorsal lorica divided by ribs into panels or facets; foot not loricate, freely movable; ventral plate with oval foot-opening under transverse distinct line; toes short, slender, pointed. Cross-section of body somewhat compressed (Fig. 14d). Male unknown.

Total length 200-255 µm, lorica 95-145 µm, width 70-90 µm, spicules 5-6 µm.

Distribution: Cosmopolitan in fresh and brackish water, rarely in the pelagic. Two localities, probably more widespread, but rare. N.S.W., Tas. 10.5-13.0°C, pH 6.7-8.4, DO 10.0 mg l⁻¹.

Literature: Koste 1978, Koste & Shiel 1980.

Genus *Trichotria* Bory de St Vincent

Trichotria Bory de St Vincent, 1827, p. 752.

Head, body and three foot-segments heavily

loricate; cross-section hexagonal (Fig. 15:1f) (see comment with *T. buchneri* for exception); most lorica borders with spicules, greater on "shoulders" if head contracted (Fig. 15:3, 4a); lorica with facets, granulated; head lorica composed of several plates; second foot segment with relatively long spines (Fig. 15:1a fsp); toes long; corona of *Euchlanis* type; trophi (Fig. 15:1d-e) maleate; red cerebral eye (Fig. 15:1a eye). Male loricate (Fig. 15:1b-c). Food algae and detritus, diatoms preferred. *Trichotria* occurs rarely in the plankton (as migrants). Seven species recognized, with many variants; five known from Australia.

Key to Species of the Genus *Trichotria*

1. Cross-section hexagonal, three foot segments... 2
- Cross-section triangular, two foot-segments
..... *T. buchneri* Koste et al.
- 2(1). Only distal end of terminal foot segment and toes projecting beyond posterior lorica margin; lorica elongated U-shape... *T. pseudocurta* Koste et al.
All three, or at least two, foot segments and toes projecting beyond lorica margin..... 3
- 3(2). Last foot joint with dorsal minute spine between the toe bases, *T. pocillum* (Müller)
No minute spine between the toe bases..... 2
- 4(3). Lateral part of dorsal lorica conspicuously large; marginal spicules of lorica directed forward
..... *T. truncata* Whitelegge
Lateral lorica not very expanded; spicules if present not directed forward, *T. tetractis* (Ehrenberg)

Trichotria buchneri Koste, Shiel & Tan

FIG. 15:1

Trichotria buchneri Koste, Shiel & Tan, 1988, pp. 120-121, Figs 3-5.

Diagnosis: Lorica of triangular cross section with median keel ending in elongated caudal spine; dorsal lorica with longitudinal rows of denticles to keel (appears granulated by light microscopy); anterior dorsal margin deep U-shaped aperture between two lateral cusps; ventral margin with a shallower U-shaped aperture projects beyond dorsal margin to level of lateral cusps (or slightly beyond tips); rectangular plates cover head, when contracted a pyramidal projection extends to or past anterior lorica margins; foot two-segmented; without spines; toes long, rigid, with acute points.

Length 160-182 µm; width to 125 µm; height to 84 µm; proximal foot segment 24 µm, distal 15 µm; toes 50 µm.

Distribution: Known only from marginal reedbeds of acid dune lakes north of Strahan, on west coast of Tasmania (I., Garela, L., Ashwood and surrounding dune pools), 17.0-20.0°C, pH 3.1-5.15, 80.6-188.4 µS cm⁻¹, 0.9 NTU.

Comment: The morphological differences between this species and congeners were noted by Koste et al. (1988), particularly the domed and keeled cross-section, caudal spine and two-segmented foot. The

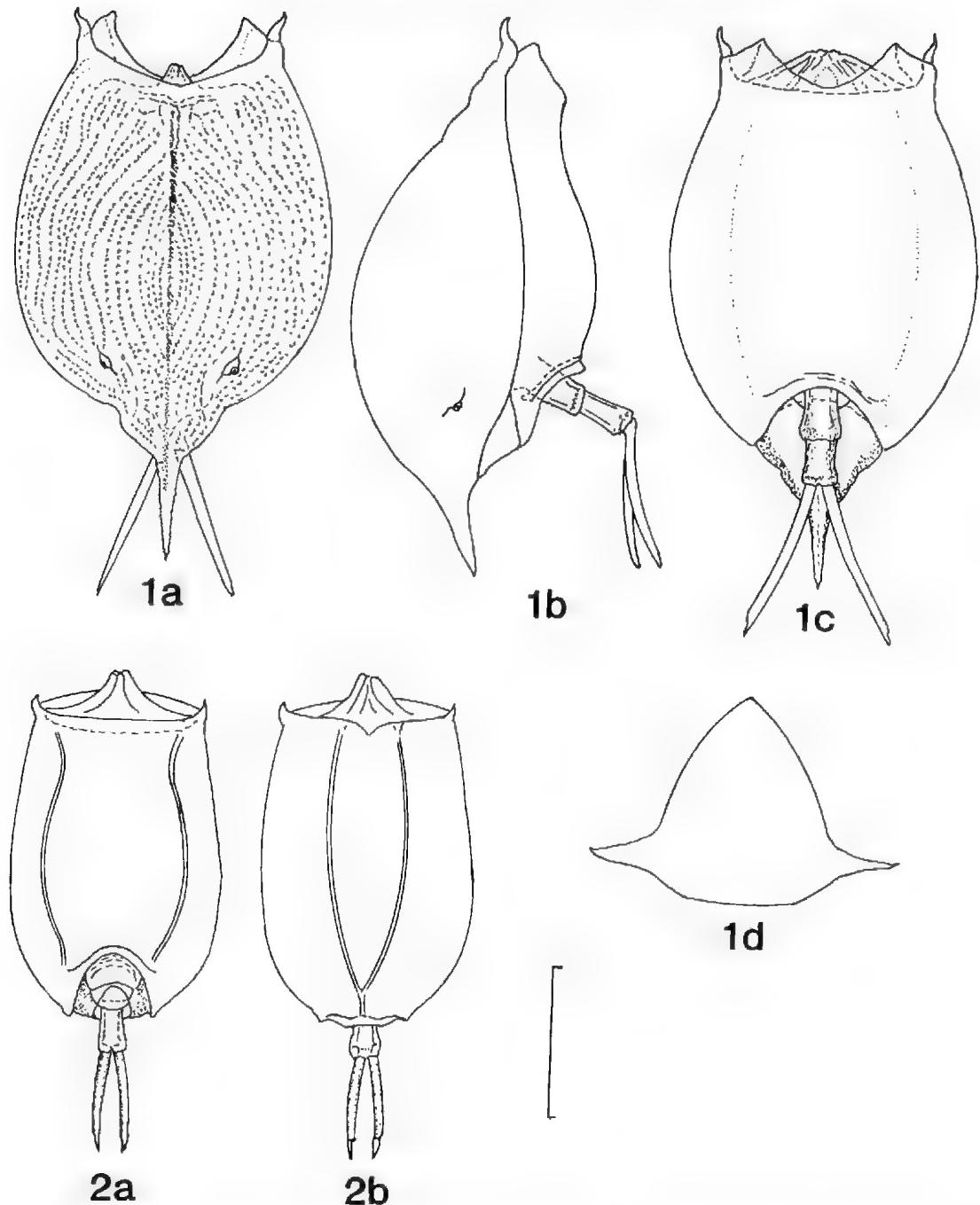
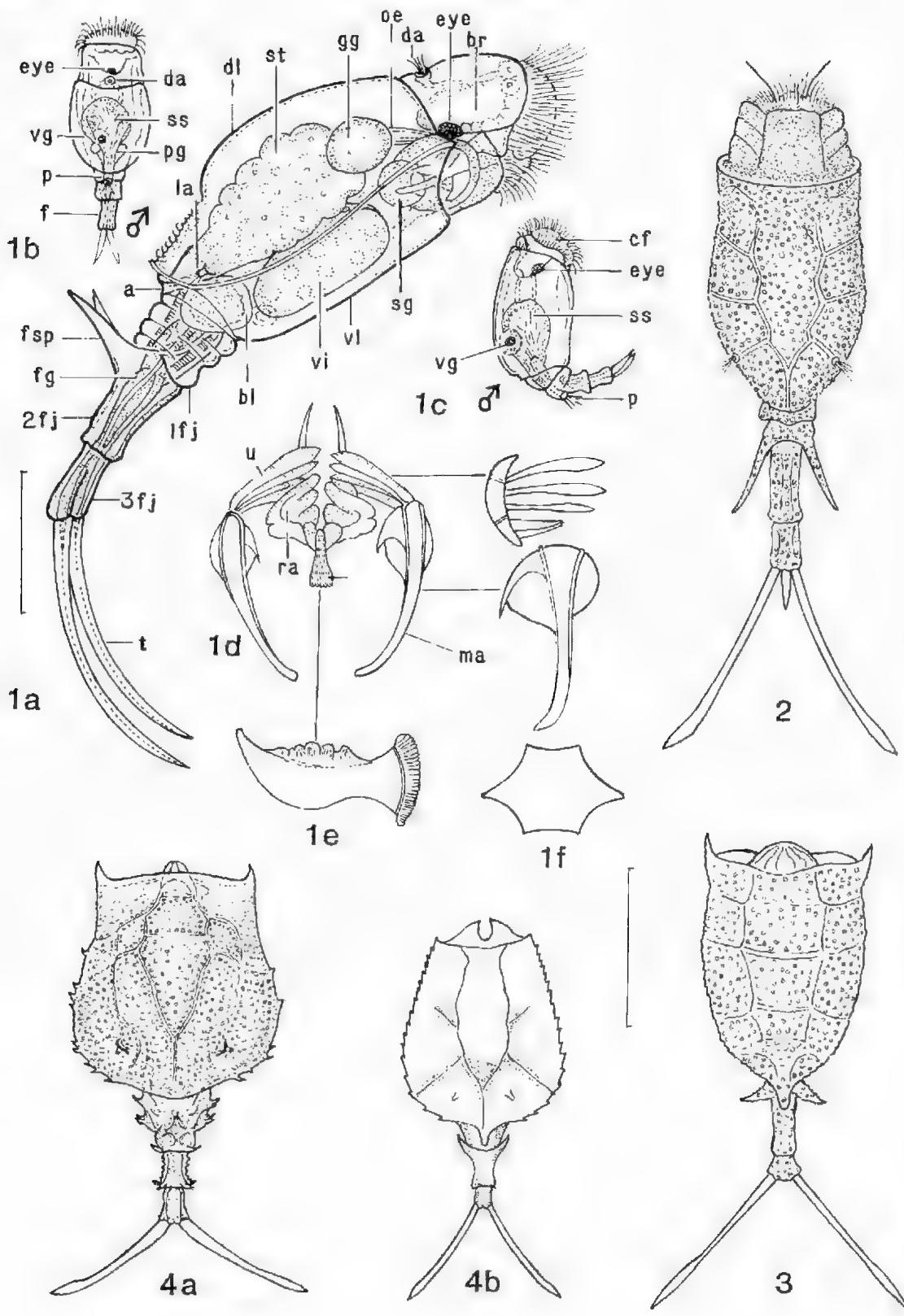


Fig. 15: 1. *Trichotria buchneri* Koste et al. a. dorsal, b. lateral, c. ventral; 2. *Trichotria pseudocurta* Koste et al. a. dorsal; b. ventral. After Koste et al. (1988). Scale line 50 μm .

armoured head is peculiarly trichotriid amongst the Rotifera, but the distinctive features of *T. buchneri* suggest that generic status may be appropriate. Accordingly, additional collections were taken at the

type locality in Jan. 1989, and additional sites for the rotifer recorded. A detailed SEM study of this species will appear at a later date (Shiel & Koste, in prep.).



Trichotria pocillum (Müller)

FIG. 16:2

Trichoda pocillum Müller, 1776, p. 281.*Dinochirus pocillum* after Ehrenberg, 1830, p. 47.*Trichotria pocillum* Bory de St Vincent, 1827, p. 752.
For extensive synonymy see Harring (1913) and Koste (1978).

Diagnosis: Length of foot segments and spine on second foot segment variable; lorica spindle-shaped, surface divided into granulated facets by ridges; corona simple, can be retracted in neck and lateral head plates; male loricate. Rare in plankton.

Length 200–300 µm (total), lorica length 110–140 µm, foot spine 53–66 µm, median minute spine on last foot segment 20–28 µm, toes 83–145 µm.

Distribution: Cosmopolitan in the littoral of fresh and brackish waters, N.S.W., Qld.

Literature: Shiel & Koste 1979.

Trichotria pseudocurta Koste, Shiel & Tan

FIG. 15:2

Trichotria pseudocurta Koste et al., 1988, pp. 121–3, Fig. 7.

Diagnosis: Lorica small, U-shaped in outline with both surfaces granulated; triangular cusps at external angles; two raised ribs on ventral surface terminate anterior to raised rim of foot opening; similar ribs form a low keel on dorsal surface, commence either side of median notch on dorsal anterior margin, fuse to a single keel on posterior lorica; foot 3-segmented, without spines; toes with short claws.

Length to 125 µm; width to 74 µm; toes to 30 µm.
Distribution: Known only from humic waters of Lake Pedder (White Spur Inlet), Tasmania, 21°C, pH 5.2, 32.6 µS cm⁻¹, 0.5 NTU. Resembles *T. curta* (Skorikow) from the Volga R., however the latter is smaller (110 µm long) with more angular morphology, and lacks the frontal cusps.

Trichotria tetractis (Ehrenberg)

FIG. 16:1, 3

Dinochirus tetractis Ehrenberg, 1830, p. 47.*Trichotria tetractis* (Ehrenberg) after Carlin, 1939, p. 40.

For extensive synonymy see Koste (1978:157).

Diagnosis: All morphological characteristics variable; lorica spinulated or not; measurements of lorica, foot segments, dorsal and ventral lorica ornamentation differ between individuals, with

Fig. 16:1, *Trichotria tetractis* (Ehrenberg); (a) female, lateral, swimming; (a = anus, bl = bladder, br = brain, dl = dorsal lorica, da = dorsal antenna, eye = cerebral eye; fg = foot gland; ff = foot segment; fsp = foot spines, gg = gastric gland, la = lateral antenna, oe = oesophagus, sg = salivary gland, st = stomach, vi = vitellarium, vi = ventral lorica); (b) male [da = dorsal antenna, eye = cerebral eye, f = foot, p = penis, pg = prostate gland, ss = testis, vg = vestigial gut]; (c) male, lateral [cf' = ciliated fields, corona, eye = cerebral eye, p = penis, ss = testis, vg = vestigial gut]; (d) trophi [ra = ramus, u = uncus, ma = manubrium]; (e) uncus, lateral; (f) lorica, cross-section; 2, *T. pocillum* (Müller), female, dorsal, swimming; 3, *T. tetractis*, contracted dorsal; 4, *T. truncata* (Whitelegge); (a) dorsal, from Canada; (b) from Romania; (T. *longispina* after Rodewald 1935) Fig. 15:1a, 1, 2, 3, 4a after Koste (1984); 4b, after Rodewald (1935). Scale lines, left 50 µm (Fig. 15:1a–c); lower right, 100 µm (2–4).

morphological series between *T. truncata* and *T. tetractis similis* (latter has very long toes; 120–190 µm (Fig. 17)); caudal part of lorica with one or paired hooks (*T. tetractis caudata*; spinules on second foot segment may be very short (*T. tetractis paupera*)).

Length typical form: 218–380 µm, toes to 160 µm; *T. tetractis similis* (Stenroos, 1898): 330–400 µm, second foot segment 42–48 µm, toes 120–190 µm; *T. tetractis caudata*: 230–260 µm, caudal hook of lorica 22–28 µm, toes 50–72 µm.

Distribution: Cosmopolitan in macrophytes, littoral. Commonly in shallow waters of billabongs in N.S.W., Qld., Vic. (typical form) and N.T. (*similis*), 13.5–24.5°C, pH 6.3–8.0, DO 5.8–9.2 mg l⁻¹, 59–400 µS cm⁻¹, 2–160 NTU.

Literature: Koste 1978, 1981, 1984; Shiel & Koste 1979; Green 1981; Berzins 1982.

Trichotria truncata Whitelegge

FIG. 16:4a–b

Dinocharis truncatum Whitelegge, 1889, p. 315.*Dinocharis intermedia* Bergendal, 1892, p. 107, Fig. 6:33.*Trichotria cornuta* Myers, 1938, p. II.*Trichotria tetrica* var. *truncata* (Whitelegge) in Koste, 1978, p. 157.

Diagnosis: Margin of lorica with spicules, also on foot segments, all directed forward; most with shorter toes as in *T. tetractis*, but many intermediate forms; variable facettation on lorica.

Length 95–146 µm, greatest width 128 µm, toes 60–100 µm.

Distribution: Acidophil, in *Sphagnum*, mainly between plants, seldom in open water, N.S.W., N.T., Vic. 25.0–28.5°C, pH 5.44–7.6, DO 6.0–6.2 mg l⁻¹, 23–145 µS cm⁻¹.

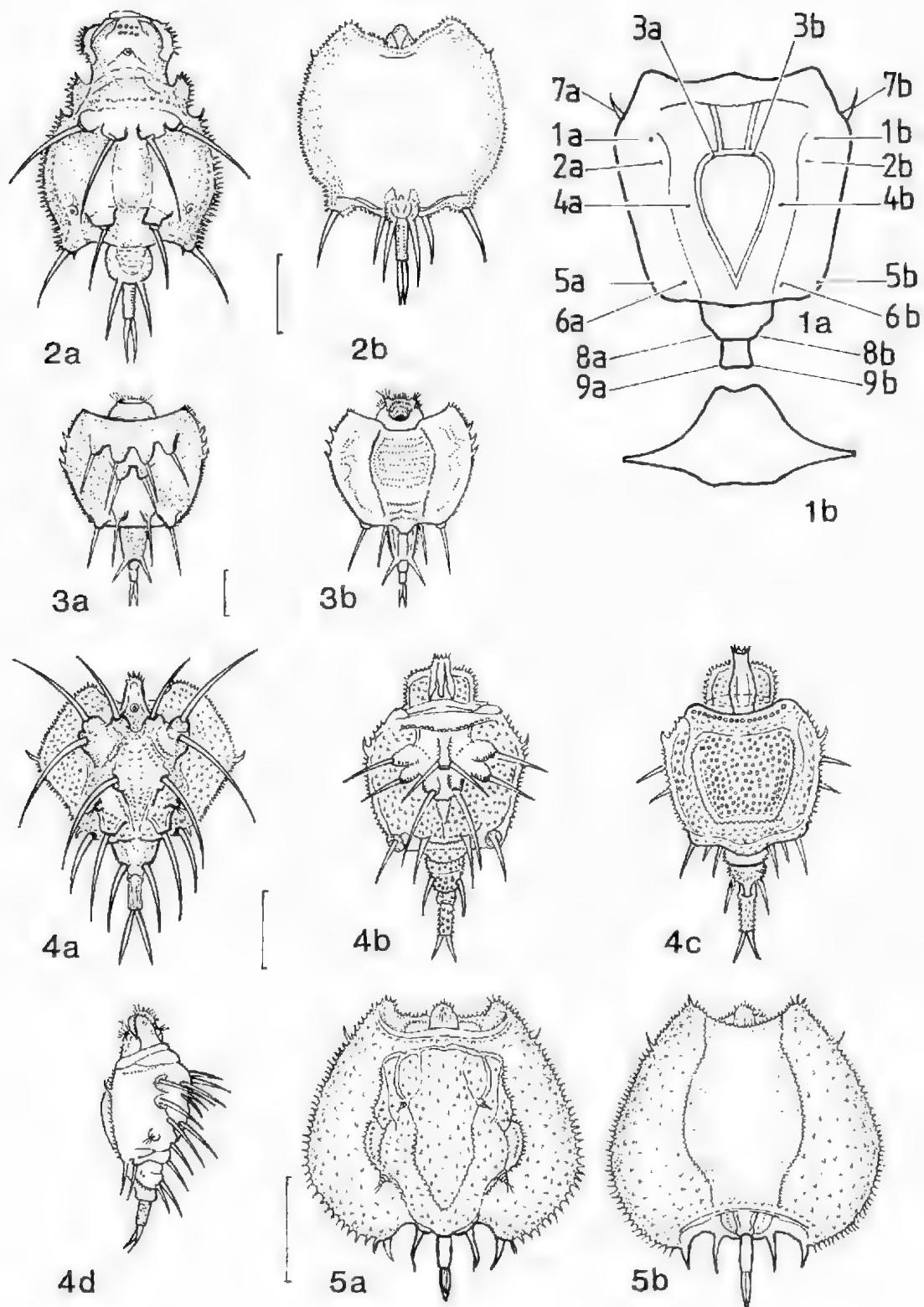
Literature: Koste 1978, 1981, 1984.

Comment: Although morphologically variable, *T. truncatum* is readily distinguished from *T. tetractis* in material we have examined from both Australian and Canadian collections (cf. Chengalath & Koste 1983), and we consider it a distinct species.

Not yet recorded from Australia

T. tetrica *caudata* (Lucks, 1912); cf. Koste 1984, p. 116;*T. tetrica* *paupera* (Ehrenberg, 1830);*T. curta* (Skorikov, 1914);*T. euknosmetra* Myers, 1934,

(See Koste, 1978, pp. 157–8 for details).



Genus *Macrochaetus* Perty

Lorica flat, hexagonal cross-section, head part retractile; lorica granulated with minute spinules; more or less developed anal section; two loricata foot segments; toes generally spindle-shaped; paired symmetrically inserted spines (Fig. 18:1a); lorica margin with spicules, shoulder hooks larger (Fig. 18:1a, 7a-b); integument opaque; corona simple, with central buccal field and longer lateral sensory hairs (Fig. 18:3b); dorsal and lateral antennae on visible papillae; one cerebral eye; mastax with malleate trophi; eggs and males unknown. All species live between or on water plants and are rare in open water.

Key to Species of the Genus *Macrochaetus*

[refer to FIG. 18:1a]

1. Only one pair of rudimentary anteriosubmedian spines present (2a, b). *M. danneeli* Koste & Shiel
More spines present 2
- 2(1). Two anterolateral spines, two anteriomedian spines, two posteriomedian spines present, central dorsal spine pair absent (4a, b) ... *M. collinsi* (Gosse)
Central dorsal spine pair present 3
- 3(2). Two anteriolateral-, two anteriomedian-, two central median- and two anteriosubmedian spines present *M. altamirai* (Arevalo)
Two anteriolateral-, two anteriomedian, two anteriosubmedian- and two posteriomedian spines present *M. subquadratus* (Perty)

Macrochaetus altamirai (Arévalo)

FIG. 18:3a, b

Polychaetus altamirai Arévalo, 1918, p. 1-47.

Macrochaetus esthonicus Riikoja, 1925, p. 7, Fig. 2j.
Macrochaetus altamirai (Arévalo) after Selga, 1952.

M. australiensis Berzins, 1982, p. 18, Figs. 17, 38.

Diagnosis: Shape, size and spicules at lorica margin variable; distinguished from *M. collinsi* only by paired central dorsal spines (see key to species).

Lorica length 80-115 µm, width 76-108 µm, toes 20-28 µm.

Distribution: Cosmopolitan warm stenotherm, rare. Probably more widely distributed in Australia than a single record from Victoria would indicate (as *M. australiensis* by Berzins 1982).

Literature: Koste 1978; Shiel & Koste 1985.

Macrochaetus collinsi (Gosse)

FIG. 18:2

Dinocharis collinsi Gosse, 1867, p. 269, Figs. 1-4.
Macrochaetus collinsi (Gosse) after Harring, 1913, p. 67.
For extensive synonymy see Koste, 1978, p. 161.



Fig. 17: *Trichotria tetractis similis*, lateral (toes 190 µm). After Koste (1984).

Diagnosis: Shape, size, length and number of spinules on margin variable; number of dorsal spines constant; lorica brownish.

Total length 94-250 µm, lorica 53-112 µm, width 62-112 µm, second foot segment 20-25 µm, toes 16-20 µm, dorsal spines 48-66 µm, posteromedian spines 24-48 µm, anal segment spines 32-35 µm.

Distribution: Pantropical and subtropical, warm stenotherm, benthic. N.T., Qld, Tas. 28.5-29.9°C,

pH 5.44-5.47, DO 5.45-6.2 mg l⁻¹, 23-44 µS cm⁻¹, alkalinity 2.6-2.7 mg l⁻¹.

Literature: Koste 1978; Shiel & Koste 1979; Tait et al. 1984.

Macrochaetus danneeli Koste & Shiel

FIG. 18:5

Macrochaetus danneeli Koste & Shiel, 1983, p. 116, Figs. 7a-d.

Diagnosis: Lorica granulated/pustulated; dorsal lorica with terraced sides to blunt keel; margin of keel base with longer spinules; uppermost keel dorsum covered with large cuticular ledges and beading; anal segment spineless; shoulder spines (Fig. 18:1a, 7a), posterolateral- (5a, b),

Fig. 18: 1 (a) points of insertion of spines and setules in *Macrochaetus* Perty spp., dorsal lorica and foot segments [1a, b = anteriolateral spines, 2a, b = anteriosubmedian spines, 3a, b = anteriomedian spines, 4a, b = central dorsal spine pair, 5a, b = posterolateral spines, 6a, b = posteriomedian spines, 7a, b = shoulder hooks, 8a, b = anal segment spines, 9a, b = foot segment]; (b) *Macrochaetus* lorica, cross section. 2, *M. collinsi* (Gosse): (a) dorsal, swimming; (b) lorica, ventral. 3, *M. altamirai* (Arevalo): (a) dorsal; (b) ventral. 4, *M. subquadratus* Perty: (a) dorsal; (b) dorsal; (c) ventral; (d) lateral. 5, *M. danneeli* Koste & Shiel: (a) dorsal; (b) ventral. Fig. 18:1a, b, 2a, b, 4a, 5a, b, after Koste & Shiel (1983); 3a, b, after Rodewald (1940); 4a-d, after Wulfert (1964). Scale lines 50 µm each number group.

posteromedian- (6a, b) and only one pair of rudimentary anterosubmedian spines present.

Lorica length 125–130 μm , width 130–137 μm , foot segment 20 μm , toes 16–18 μm .

Distribution: Single locality known: Buffalo Billabong, Magela Creek, N.T. 30.9°C, pH 5.38, DO 4.15 mg l⁻¹, 29 $\mu\text{S cm}^{-1}$.

Macrochaetus subquadratus Perty

FIG. 18:4a–c

Macrochaetus subquadratus Perty, 1850, p. 22.

Polychaetus subquadratus Perty, 1852, p. 45, Fig. 1:6.

Diagnosis: Lorica generally hexagonal (Fig. 18:4a); ten dorsal spines of variable size and shape; shoulder spines most conspicuously large.

Lorica length 80–135 μm , width 73–140 μm , second foot segment 8–16 μm , toes 15–22 μm .

Distribution: Cosmopolitan in periphyton of aquatic macrophytes. Rare migrant in plankton, more common in billabongs. Thermophile.

Literature: Koste 1978; Shiel & Koste 1979; Green 1981.

Not yet recorded from Australia

M. hauerianus Wulfert 1964 (=*M. collinsi* var. Hauer 1938), p. 534 (Indonesia);

M. longipes Myers 1934, p. 13; see Koste 1978 p. 161;

M. multispinosus Myers 1934, p. 12; recorded from the neotropics and S. Nearctic;

M. philopax Wulfert 1961, p. 87; single find in central Germany;

M. sericus (Thorpe) 1893, p. 182; see Koste 1972, Koste & Shiel 1983 p. 117 Fig. 8.

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BRIEF COMMUNICATION

REDISCOVERY OF *UPEROLEIA ORIENTALIS* (PARKER)
(ANURA: MYOBATRACHINAE)

Glauertia orientalis was described from three male frogs collected by W. H. Stalker in 1905 on Alexandria Station ($19^{\circ}08'$, $136^{\circ}43'$ *vide*¹) on the Barkly Tableland, Northern Territory, and a female frog collected by G. H. Wilkins in 1925 from Groote Eylandt¹.

The species was referred to *Glauertia* Loveridge because of its moderately extensive webbing on the toes (Fig. 1) and its widely exposed frontoparietal fontanelle.



Fig. 1. Plantar view of the foot of *Uperoleia orientalis* (Holotype, Alexandria Station).

Glauertia orientalis has been reported over a wide range in the north of Australia^{2,3,4}. The genus was referred to the synonymy of *Uperoleia*⁵ when it was shown that the generic characters represented extremes in continua expressed within *Uperoleia*. *U. orientalis* was redescribed from the holotype and topotypic paratypes⁵ but the Groote Eylandt paratype was not examined at that time. Its conspecificity was called into question because of distribution and other data provided in the generic revision⁵. No other referable material was available to these authors.

Later collecting⁶ failed to produce further specimens of *U. orientalis* at the type locality, and further studies on Groote Eylandt resulted in the female paratype being referred to *U. inundata* Tyler, Davies & Martin.⁷

Uperoleia orientalis thus remained known only from the type locality and from the holotype and two topotypic paratypes.⁸

Whilst examining a collection of *Uperoleia* from the Northern Territory Museum (NTM), I found a specimen referable to *U. orientalis*.

The frog (NTM RA88) was collected by Mike Gillam during the Cox River Survey on 2.7.1977 adjacent to the Arnold River ($15^{\circ}43'$, $134^{\circ}37'$), at night in paperbark woodland (*Melaleuca* spp) in a spring-fed swamp. The species was abundant at the locality⁹.

The specimen is small (probably sub-adult) with a snout-vent length of 17.6mm. Toe webbing is moderately extensive (characteristic of the species) and there are very prominent subarticular and supernumerary palmar tubercles on the hands. The head is small in proportion to the body and the parotoid glands are prominent. Inguinal and coccygeal glands are extensive and coalesce. No mid-vertebral stripe is apparent.

The site of collection represents a range extension of about 500 km to the north north-west.

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**THE OCCURANCE OF PLANT PARASITIC NEMATODES IN THE ARID
REGION OF SOUTH AUSTRALIA**

BY JACQUELINE M. NOBBS

Summary

THE OCCURRENCE OF PLANT PARASITIC NEMATODES IN THE ARID REGION OF SOUTH AUSTRALIA

There is little information on the occurrence of plant parasitic nematodes in arid South Australia. Twenty-four genera of plant nematodes from the area encompassing the Northern Flinders Ranges to Cape Jervis have been identified together with a relationship between the distribution of plant species and the distribution of plant nematodes¹. The distribution of plant species was related to rainfall. Following on from this work, a survey of the arid region (mean annual rainfall less than 250mm) was undertaken over a four year period (1983–1986).

The soil was sampled from under native vegetation, the nematodes extracted using a modified Baermann's funnel technique² and where possible the nematodes identified to species level. At many sites few mature female specimens were extracted, so identification to genus only was possible (Table 1).

There were several genera of fungal feeding tylenchids identified which included *Aphelenchus avenae*, *Aphelenchodes* sp., *Coslenchus* c.f. *costatus*, *Neotylenchus* s.l., *Tylenchus* s.l. and *Ditylenchus* sp. These are not included with the plant nematodes in Table 1. Twelve genera of plant nematodes were identified from the arid region as well as juveniles and males of the Heteroderidae which were not identifiable because of the absence of females or cysts.

The most widely distributed plant nematode was *Tylenchorhynchus tobari* (Sauer & Annells, 1981). Of the 374 sites sampled, 63% contained *T. tobari*. All other species occurred at less than 8% of the sites. More than one taxon was present in 26% of the sites and a similar percent of sites had no plant nematodes present. The arid

regions are an adverse environment for most organisms. To survive, organisms must be drought resistant and also respond rapidly to the stimulus of rainfall. Some nematodes are ideally suited to the arid region as they can form an anhydrobiotic state in which metabolic respiration is greatly reduced but are quick to revive with addition of water³ and begin to reproduce rapidly after revival.

T. tobari (Sauer & Annells, 1981) is a widely distributed nematode within the region and must be well adapted to the environment. The species was first described from a site near Wentworth, N.S.W.⁴. The species was cultured by planting seeds of certain species of Chenopodiaceae (a common family in arid Australia) into soil known to contain *T. tobari*.

Studies of host/parasite relationships and environmental effects on nematode population growth will be presented in detail in another paper.

¹ Reay, F. & Wallace, H. R. (1981) *Nematologica* 27, 319–329.

² Schindler, A. E. (1961) *Plant Disease Reporter* 45, 747–748.

³ Freckman, D. W., Whitford, W. G. & Steinberger, Y. (1987) *Biology and Fertility of Soils* 3, 3–10.

⁴ Sauer, M. R. & Annells, C. M. (1981) *Nematologica* 27, 422–431.

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TABLE 1. Number and percent of sites from which plant nematodes (PP) were extracted in the years 1983 to 1986 inclusive.

Genus and Species	Sites-Sampled	Percent of Total Sites
<i>Tylenchorhynchus tobari</i> Sauer & Annells, 1981	237	63.3
<i>Pratylenchus</i> sp.	24	6.4
<i>Morulaimus</i> sp.	16	4.3
<i>Helicotylenchus</i> sp.	16	4.3
<i>Scutellonema</i> sp.	16	4.3
<i>Radopholus</i> sp.	14	3.7
<i>Tylenchorhynchus velatus</i> Sauer & Annells, 1981	12	3.2
<i>Tylenchorhynchus</i> sp.	12	3.2
<i>Ratylenchus</i> sp.	7	1.9
<i>Hoplolaimus</i> sp.	7	1.9
<i>Morulaimus geniculatus</i> Sauer, 1966	5	1.3
<i>Paralongidorus</i> sp.	4	1.1
Heteroderidae males and juveniles	3	0.8
<i>Scutellonema laeviflexum</i> Phillips, 1971	3	0.8
<i>Tylenchorhynchus unnutatus</i> (Cassidy, 1930) Golden, 1971	3	0.8
<i>Scutellonema minutum</i> Sher, 1964	2	0.5
<i>Tetramesorus hastulatus</i> (Golden, 1960) Siddiqi, 1963	1	0.3
<i>Helicotylenchus variabilis</i> Phillips, 1971	1	0.3
<i>Radopholus crenatus</i> Colbran, 1971	1	0.3
<i>Paratylenchus</i> sp.	1	0.3
<i>Hemicyphophora</i> sp.	1	0.3
Total number of sites sampled	374	100.0
Sites with >1 genera of PP	97	25.9
Sites with PP	276	73.8
Sites without PP	98	26.2

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ROTIFERA FROM AUSTRALIAN INLAND WATERS IV. COLURELLIDAE (ROTIFERA:MONOGONONTA)

*BY W. KOSTE**, & *R. J. SHIEL†*

Summary

Diagnostic keys are given to genera and species of the rotifer family Colurellidae (*Colurella*, *Squatinella*, *Lepadella*, *Heterolepadella*) recorded from Australian inland waters. All species are figured and available distribution data and ecological information given. Some widely-distributed taxa not yet recorded from the continent are included.

KEY WORDS: Rotifera, taxonomy, Australia, known species, Colurellidae

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Introduction

The monogonont rotifer families considered to date in our revision of the Australian Rotifera (Koste & Shiel 1986b, 1987b, 1989) have included the most common planktonic taxa in Australian inland waters. Here we review the Australian representatives of the family Colurellidae, several genera of which have widely-distributed species in plankton and littoral collections in Australian waters and are considered hekoplankters (*sensu* Hutchinson 1967) rather than accidental incursions, i.e. pseudoplankton (= lyphoplankton of Ruttner-Kolisko 1974) (e.g. *Lepadella patella*). In general, however, the Australian representatives of the Colurellidae (*Colurella*, *Squatinnella*, *Lepadella*, *Heterolepadella*) are littoral (epiphytic or epibenthic) in habit. They are encountered commonly in the shallow vegetated areas of billabongs and other wetlands, where diverse macrophyte associations effectively partition the habitat, providing abundant micropishes.

Diagnostic keys, brief descriptions and figures of all known Australian representatives of the family are provided to enable identification to species. Some widely distributed taxa not yet recorded from Australia are included. The format follows that of earlier parts; dichotomous keys are followed by individual species' descriptions and known Australian records. Relative abundance is indicated by: "common" (more than 30 widely dispersed records), "uncommon" (10-30 localities), "rare" (<10 records). Brief ecological data are included where available. Early Australian records cited in Shiel & Koste (1979) are not repeated here, nor are the majority of northern hemisphere citations given by Koste (1978), which contains a detailed treatment

of the Rotifera outside Australia. Keys to families are included in Koste & Shiel (1987b).

Family Colurellidae Bartos

Loricate rotifers, the corona in all genera with a membranous cap or semicircular shield (retractile in all except *Squatinnella*); no lateral sulci; *Colurella* and *Paracolurella* with ventral sulcus; trophi malleate; ventral plate with caudal foot-opening or enlarged for basal foot segment; toes slender, sharply pointed. Four genera: *Colurella*, *Lepadella*, *Squatinnella*, *Paracolurella*.

Key to genera of the Family Colurellidae

1. Lorica laterally compressed, with ventral or dorsal and ventral apertures (Fig. 2).....
Lorica dorso-ventrally flattened, without such apertures.....
2(1). Lorica a single structure, with ventral aperture (Fig. 1).....*Colurella* Bory de St Vincent
Lorica two plates, with dorsal and ventral apertures (Fig. 2:8).....*Paracolurella* Myers (not known from Australia).
3(1). Hood or head-shield large, non-retractile (Fig. 3).....*Squatinnella* Bory de St Vincent
Hood small, retractile (Fig. 5).....
.....*Lepadella* Bory de St Vincent

Genus *Colurella* Bory de St Vincent

Coluria Bory de St Vincent, 1824, p.203.

One-piece lorica, in lateral view oval, egg- or hatchet-shaped (outline of lorica differs according to degree of contraction, particularly ventral margin); anterior lorica margin more or less truncated or rounded; posterior margin rounded, gradually merging into blunt, straight or curved projections, in some cases sharply pointed, offset with-like extensions of posterior margin (Fig. 1c);

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ventral cuticle between mussel-like lorica borders delicate, membranous, may be distorted in preservative; corona of the *Euchlanis* type (cf. Koste & Shiel 1987b); foot with three or four segments, basal segment mostly pliable and often of indistinct structure; distal foot segment (before toe) with dorsal sensory pore; toes of variable length, species with long toes more compressed laterally; toes separate, however may appear fused as frequently are stuck together; gastric glands mononucleate; trophi malleate; eyeless or with two eyespots, which may or may not be red-pigmented; lateral antennae very conspicuous; male little known and insufficiently described. Resting eggs retained in lorica of parent on death (cf. Fig. 2:3d).

Variability in the described species requires investigation, particularly whether the morphology of different races ("var.") or forms represents

ecotypic variation ["Millienfaktoren" (Hauer 1924)], e.g. the variability in the lorica ends in *C. uncinata* or *C. adriatica*. Ecotypic variation is common in the Australian brachionids (Koste & Shiel 1987b), and variants are known in the five species of *Colurella* recorded from Australia. It is likely that other species occur here; in view of their small size (most <100 µm) colurellids are easily overlooked in detritus-rich samples.

Key to species of the Genus *Colurella*

- 1. Lorica surface smooth..... 2
- Lorica surface with longitudinal furrows or facets *C. tessellata* (Glascott)
- 2(1). Lorica valve (lateral) slender, posteriorly with variable apices 3
- Lorica valve rounded, plump *C. obtusa* (Gosse)

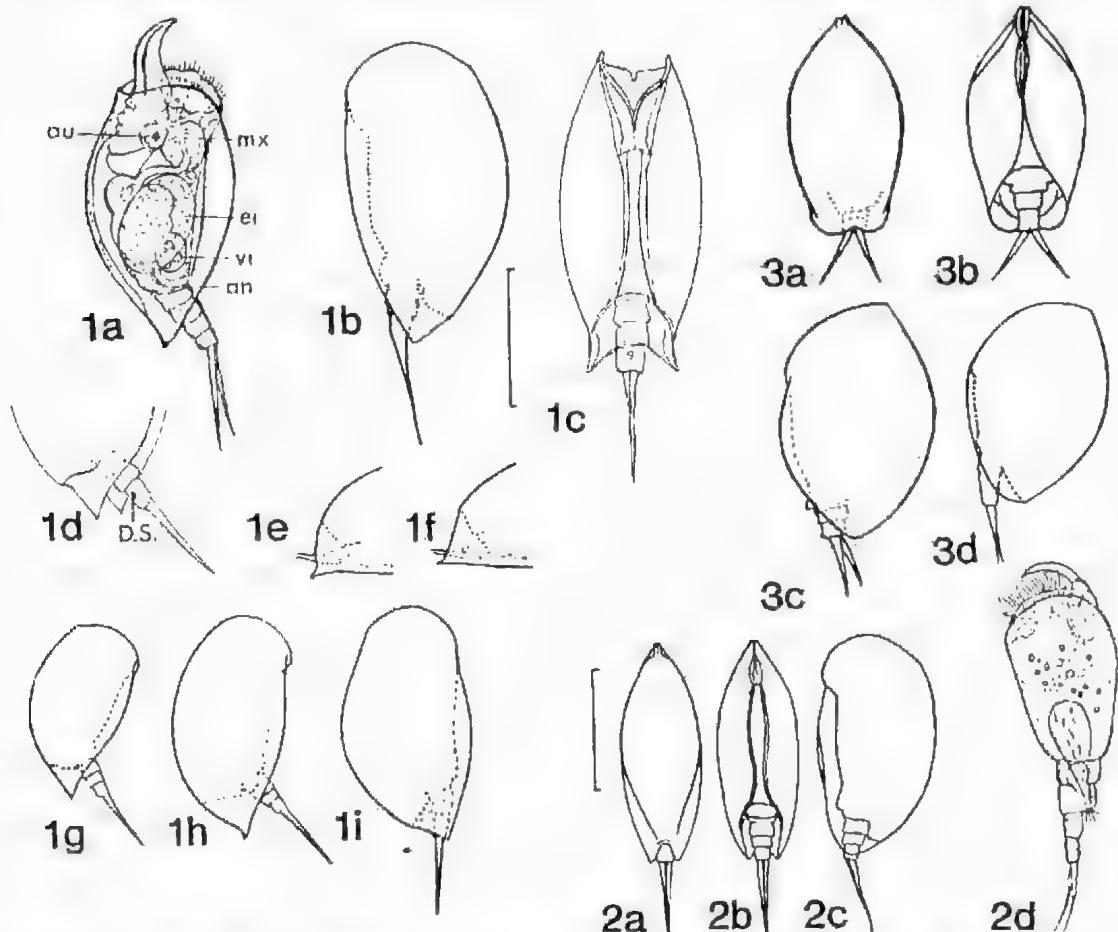


Fig. 1H. *Colurella adriatica* (Ehrenberg): (a) lateral fan - anus; au - eye; ei - subitaneous egg; mx - maxilla; vi - vitellarium; (b) lateral, contracted; (c) ventral; (d) posterior lorica showing foot and toe (D.S. - dorsal sensory pit); (e-i) lateral views showing variation in lorica morphology. 2. *C. colurus* (Ehrenberg): (a) dorsal; (b) ventral; (c) lateral; (d) male; lateral. 3. *C. obtusa* (Gosse): (a) dorsal; (b) ventral; (c) lateral; (d) another morph, lateral. 1a, after Corda (1838); 1b, 3d, after Carlin (1939); 1c, d, after Wulfert (1950); 1e-i, 2a-c, after Hauer (1925); 2d, after Wiszniewski (1953); 3a-c, after Hauer (1924). Scale lines 50 µm.

- 3(2). Posterior end of lorica with raised lines terminating in variable tapering, downward-curving (occasionally lightly upward-curving) spines; lorica high (length/height ratio <1.8); toes short
C. uncinata (Müller)
 Posterior end of lorica broadly rounded, or blunt-spined or tapering, lorica low (ratio >1.8); toes long 4
 4(3). Lorica valve posteriorly rounded, or at most extended to a blunt apex (Fig. 1:2c).
C. colurus (Ehrenberg)
 Lorica valve posteriorly with curved spines (Fig. 1:4c)
 *C. adriatica* Ehrenberg

Colurella adriatica Ehrenberg
FIG. 1:1

Colurella adriatica Ehrenberg, 1831, Fig. 3:3.

Diagnosis: Extremely variable lorica size and phenotype, particularly points at posterior end of lorica. These are the only features separating *C. adriatica* from *C. colurus*. Pejler (1962) noted transitional forms. Different ecotypes were described by Hauer (1924), with increased lorica size and toe length correlated with increasing salinity. The measurements below encompass the range of ecotypes (Koste 1978).

Length 85–113 µm; width 29–48 µm; height 44–66 µm; toe length 28–48 µm.

Distribution: Probably cosmopolitan. Euryhaline; Rare: fresh and slightly saline waters of southeast S. Aust., Tas. and western Vic. Berzins (1982) recorded *C. adriatica* as widely distributed in eastern Australia. 5.0–30.0°C, pH 5.5–10.5, dissolved oxygen (DO) 6.0–11.2 mg l⁻¹, conductivity (K₂₅) 57–13,940 µS cm⁻¹ turbidity 21–67 nephelometric turbidity units (NTU).

Literature: Ridder 1972; Koste 1978.

Colurella colurus (Ehrenberg)
FIG. 1:2

Monura colurus Ehrenberg, 1830, p. 44.

Colurella colurus after Harring, 1913, p. 29.

Diagnosis: Distinguished from *C. adriatica* only by the rounded or blunt-spined posterior lorica. Resting egg and male known (Fig. 1:2d).

Length 71–110 µm; width 25–37 µm; height 39–55 µm; toe length 25–40 µm.

Distribution: Cosmopolitan, widely tolerant, occurring in fresh, euryhaline saline and coastal waters. European temperature 1.0–28.0°C and pH 4.9–10.0. Ridder (1972) records *C. colurus* from 15,035 g Cl⁻. Rare: Tas., Vic. 11.8–16.0°C, pH 5.7–6.4, 415–2130 µS cm⁻¹.

Literature: Koste 1978.

Colurella obtusa (Gosse)

FIG. 1:3

Colurus obtusus Gosse in Hudson & Gosse, 1886, p. 113, Fig. 26:3.

Colurella obtusa after Hofsten, 1909, p. 84.

Diagnosis: Lorica outline plump; margin of head-aperture directed obliquely from ventral lorica; ventral lines variable; head width approx. half lorica length, or smaller; eyespots with or without pigment.

Length 60 µm; width 28 µm; toes 17 µm.

Distribution: Cosmopolitan between aquatic macrophytes; pancontinental, uncommon, 8.0–29.0°C, pH 3.4–7.5, DO 11.2 mg l⁻¹, 36.4–1600 µS cm⁻¹, 15 NTU.

Literature: Evans 1951; Koste 1978, 1981; Shiell & Koste 1979; Green 1981; Koste et al. 1988.

Colurella tesselata (Glascott)

FIG. 2:1

Colurus tesselatus Glascott, 1893, p. 74.

Colurella tesselata after Hofsten, 1909, p. 84.

Diagnosis: Lorica with dorsal keel; facet-like pattern with ribs on lorica surface; toes relatively short.

Length 55–64 µm; width 24–31 µm; height 32–41 µm; toes 18–27 µm.

Distribution: ?Cosmopolitan (not recorded from N.Z.), sporadic in oligotrophic waters, mostly in moss, also in psammion. Single record from Coghills Creek, Tourello, Vic.

Literature: Koste 1978; Berzins 1982.

Colurella uncinata uncinata (Müller)

FIG. 2:2

Brachionus uncinatus Müller, 1773, p. 134.

Colurella uncinata after Harring, 1913, p. 30.

Diagnosis: Lorica posterior end gradually merges into downward-curving short spines; head-opening smaller than greatest lorica height.

Length 77–106 µm; width 30 µm; height to 60 µm; toes 18–23 µm; male 50–85 µm.

Distribution: Cosmopolitan, euryhaline. Common: pancontinental, 8.5–24.5°C, pH 4.8–8.0, DO 7.8–11.2 mg l⁻¹, 20–1600 µS cm⁻¹, 3–160 NTU.

Literature: Koste 1978.

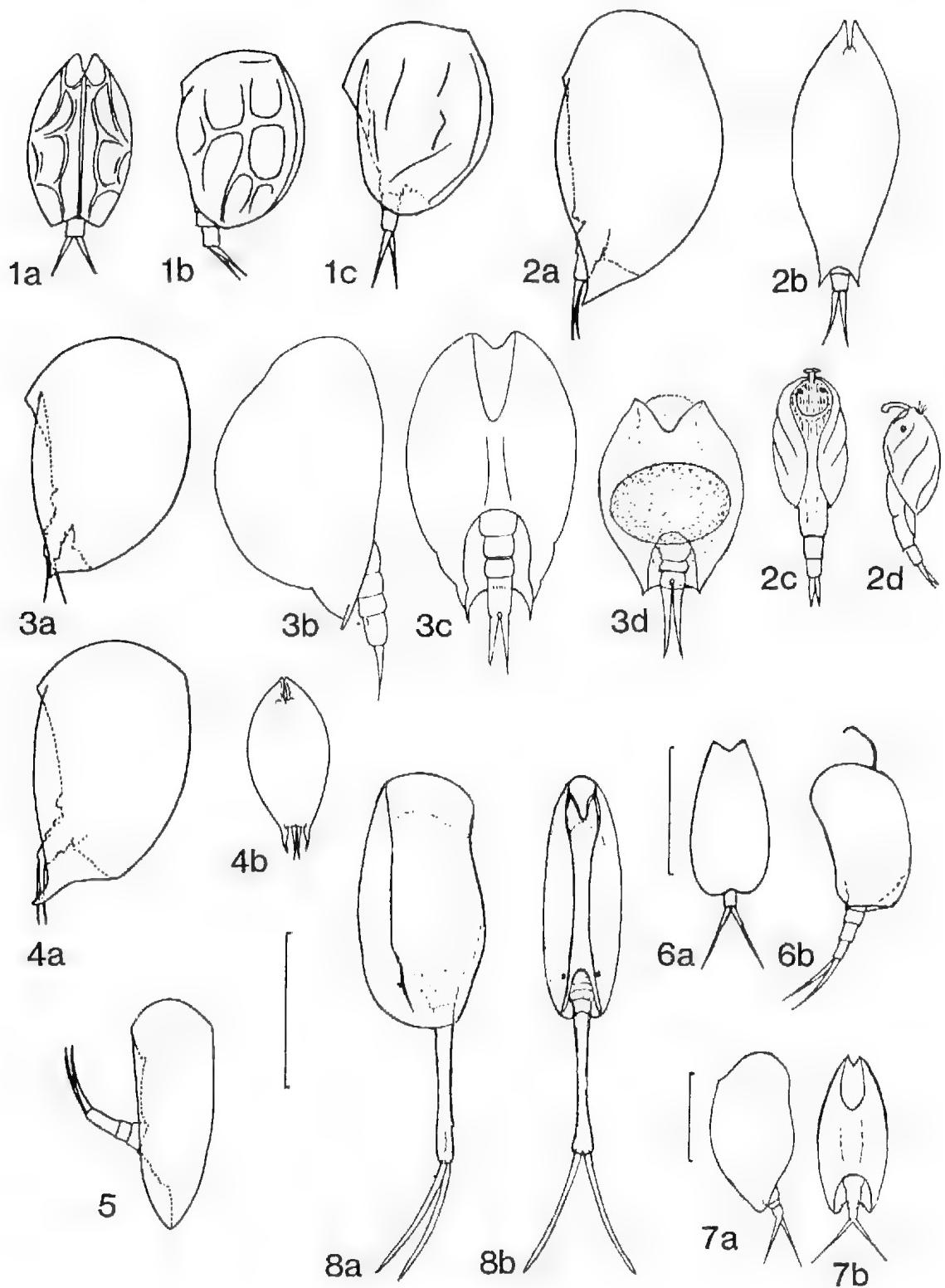
Comments: Two morphologically distinguishable taxa described originally as distinct species, but regarded by Koste (1978) as "form" variants of *C. uncinata* also are known from Australia.

Colurella uncinata bicuspidata (Ehrenberg)

FIG. 2:3

Colurus bicuspidatus Ehrenberg, 1832, p. 129.

Colurella uncinata f. *bicuspidata* after Meuche, 1939, p.



Diagnosis: Lorica width up to twice that of nominate species; highest extension of lorica at head-opening; lorica ends short, most curve downwards; toes relatively short; resting egg with punctiform cavities.

Length 60–108 µm; width 53–62 µm; height to 60 µm; toes 13–27 µm.

Distribution: Cosmopolitan in littoral of fresh and eutrophic saline waters, also marine littoral. Uncommon: N.S.W., Qld, S. Aust., Tas., Vic. 10.0–23.5°C, pH 4.5–7.5, 53–927 µS cm⁻¹.

Literature: Koste 1978; Shiel & Koste 1979; Green 1981; Berzins 1982.

Colurella uncinata deflexa (Ehrenberg)

FIG. 2:4

Colurus deflexus Ehrenberg, 1834, p. 203.

Colurella uncinata f. *deflexa* after Meuche, 1939, p. 410.

Diagnosis: Lorica end robust, elongated, turned outward, most directed ventrally. Very variable. Length 60–100 µm; width to 55 µm; height 35–55 µm; toes 17–25 µm.

Distribution: Cosmopolitan, sporadic, euryhaline. Rare: Qld, Tas. 9.5–20.0°C, pH 6.5.

Literature: Shiel & Koste 1979; Koste & Shiel 1987a.

Not recorded from Australia:

- C. denticauda* Carlin, 1939. Scandinavia
- C. dicentra* (Gosse, 1887). N. Europe; marine
- C. hindenburgi* (Steinecke, 1917) (Fig. 2:6). Probably cosmopolitan
- C. geophilus* Donner, 1951. Europe
- C. marinovi* Althaus, 1957. Black Sea, mesopelagic
- C. monodactylus* Althaus, 1957. Black Sea
- C. muellerianum* Ahlstrom, 1938. U.S.A.
- C. oblonga* Donner, 1943. Europe
- C. oxycauda* Carlin, 1939. Scandinavia
- C. paludosa* Carlin, 1939. U.S.S.R.
- C. salina* Althaus, 1957 (Fig. 2:7). Europe, N.Z.
- C. sinistra* Carlin, 1939. Europe
- C. sulcata* (Stenoos, 1898) (Fig. 2:5). Probably cosmopolitan, warm stenotherm, acidophil.
- C. unicauda* Eriksen, 1968. N. Europe.

Genus *Squatinnella* Bory de St Vincent

Squatinnella Bory de St Vincent, 1826, p. 87.

Body cylindrical to ovoid; head and corona under hyaline semicircular shield (Fig. 3:1), which is pointed apically in some species, also with

triangular side plates ("ears"); dorsal lorica smooth, also with occasional symmetric longitudinal ribs; ventral lorica smooth, with attached shield-like plate, with one or two scales, or also with keel; posterior lorica rounded, truncated or tapered to variable points; some species with long dorsal spine; short spine in median line of posterior lorica may be present; foot 2- or 3-segmented with long pointed toes; small thin spine may be present at base of toes (Fig. 3:1e); symmetric malacate trophi (Fig. 3:6); gut without peculiarities; dorsal and ventral antennae small; two widely separated distinct eyespots with crystalline bodies. Male and resting egg not yet described. Ecology of *Squatinnella* little known. Koste (1978:174) notes genus restricted to littoral, with some spp. acidophils. Four species recorded from Australia. For details of other species and variants, see Koste (1978:175–179).

Key to species of the genus *Squatinnella*

1.	With dorsal spine.....	2
	Without dorsal spine.....	3
2(1).	Foot 3-segmented; short spine at base of toes.....	<i>S. longispinata</i> (Talem)
	Foot 2-segmented; spine absent.....	<i>S. levigata</i> (Zacharias)
3(1)	With a short spine above the base of the toes.....	<i>S. rostrum</i> (Schmarda)
	Without spine above toe bases.....	<i>S. mutica</i> (Ehrenberg)

Squatinnella longispinata (Talem)

FIG. 3:3

Stephanops longispinus Talem, 1867, p. 252, Pl. 10, Figs 1–3.

Squatinnella longispinata after Harring, 1913, p. 96.

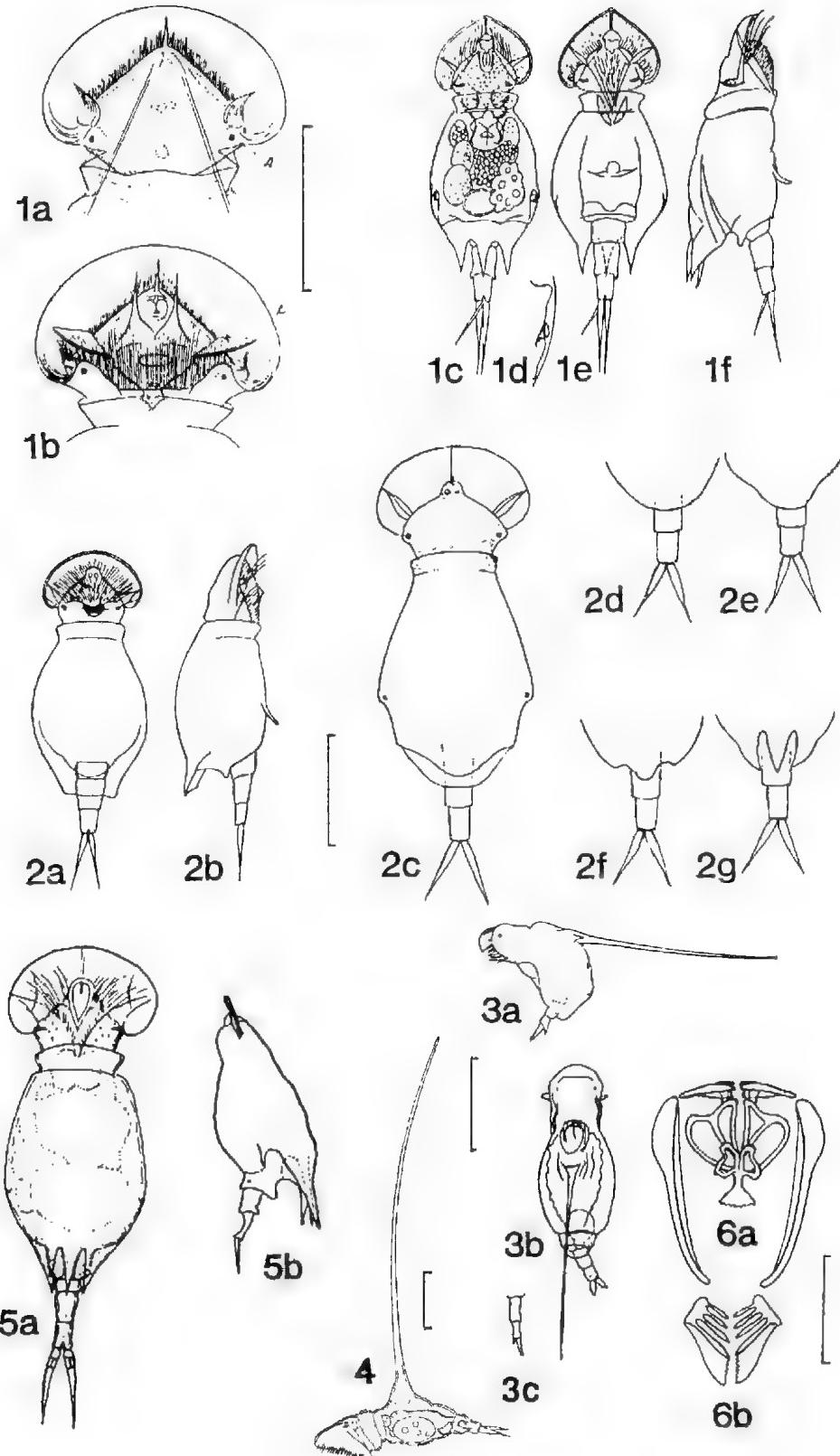
Diagnosis: Characteristic long, thin and curved dorsal spine. Pejler (1962) noted two short spines flanking dorsal spine (Fig. 3:3a). Ventral side sometimes wrinkled. Ratio dorsal spine:body length 0.8. Foot three-segmented.

Length 82–160 µm; dorsal spine 96–116 µm; toes 3–10 µm; spine(s) at the base of the toes 4–5 µm.

Distribution: Widespread but rare, mostly in moor waters between *Sphagnum* (Koste 1978). We have not encountered this species in >2000 collections, however it was recorded by Whitelegge (1889) from N.S.W., also by Evans (1951) from Victorian waters.

Literature: Pejler 1962; Koste 1978.

Fig. 2:1, *Colurella tessellata* (Glascott): (a) dorsal; (b, c) lateral. 2, *C. uncinata uncinata* (Müller): (a) lateral; (b) dorsal; (c) male, ventral; (d) male, lateral. 3, *C. uncinata bicuspisata* (Ehrenberg): (a) lateral; (b) another morph, lateral; (c) ventral; (d) ventral, with resting egg. 4, *C. uncinata deflexa* (Ehrenberg): (a) lateral; (b) habit, dorsal. 5, *C. sulcata* (Steinecke), lateral. 6, *C. hindenburgi* Steinecke: (a) dorsal; (b) lateral. 7, *C. salina* Althaus: (a) lateral; (b) ventral. 8, *Paravolturella ligumia* Myers: (a) lateral; (b) ventral. 1a, b, 2b, 4b, after Hauer (1924); 1c, 2a, 3a–c, 4a, 5, after Carlin (1939); 2c, d, after Weber (1898); 3d, 8a, b, after Koste (1978); 6a, b, after Steinecke (1917); 7a, b, after Althaus (1957). Scale lines 50 µm.



Squatinella leydigii longiseta (Pourriot)
FIG. 3:4

Squatinella leydigii f. *longiseta* Pourriot, 1971, pp. 99–100.
FIG. 3.

Diagnosis: Robust body; dorsal spine longer than body; two foot segments; no spine on distal end of terminal segment (at base of toes). Much larger animal than *S. longispinata*.

Body length 210–235 μm ; dorsal spine 270–378 μm ; ratio spine:body length 1.6; toes to 37 μm .

Distribution: Rare in submerged *Sphagnum*, *Myriophyllum*, etc. Single record from a pool near L. Gareia, western Tas. 17.0°C, pH 3.1, 80.6 $\mu\text{s cm}^{-1}$.

Comment: The nominate *S. leydigii* is not recorded from Australia. It is distinguished from *S. longispinata* by foot morphology and from the ssp. *longiseta* by its markedly smaller dimensions (body length 110–130 μm ; dorsal spine 90–110 μm ; spine:body ratio 0.8–0.95; toes 10 μm).

Literature: Koste 1978.

Squatinella mutica (Ehrenberg)
FIG. 3:2

Stephamops muticus Ehrenberg, 1832, p. 138.
Squatinella mutica after Herring, 1913, p. 97.

Diagnosis: Caudal margin of dorsal lorica semi-circular, tongue-shaped, three-lobed, with three short spines or truncate (Fig. 3:2d–g). All forms may occur in same population. Foot three-segmented.

Body length 100–226 μm ; headshield width 60 μm ; toes to 30 μm .

Distribution: Europe, N.Z. Rare, from billabongs, ponds or dams; N.S.W., N.T., Tas., Vic. 16.5–24.5°C, pH 3.8–5.3, 45.5–46.2 $\mu\text{s cm}^{-1}$.

Literature: Russell 1961; Koste 1978; Berzins 1982; Koste & Shiel 1987.

Squatinella mutica tridentata (Fresenius)
FIG. 3:5

Stephanops tridentatus Fresenius, 1858, p. 218, Pl. 10, Fig. 11.

Squatinella mutica tridentata after Wiszniewski, 1953, p. 401.

Diagnosis: Posterior lorica oval, terminating in three pointed, elongated spines of variable length.

Resembles *S. rostrum*, but lacks spine at base of toes. Headshield semicircular.

Body length 134–190 μm ; toes 20–30 μm .

Distribution: Ponds and pools, often abundant in *Sphagnum*, pH 4.8–6.2. Rare; Qld, N.S.W., Vic.

Literature: Evans 1951; Koste 1978.

Squatinella rostrum (Schmidta)
FIG. 3:1

Lixiron rostrum Schmidta, 1846, p. 20, Pl. 2, Fig. 3.

Squatinella rostrum after Carlin-Nilson, 1939, p. 3.

Diagnosis: Caudal lorica with three long or short pointed processes which arise from narrow bases. Lateral antennae sunken in dorsal lorica margins.

Length 150–217 μm ; toes 24–28 μm ; headshield to 76 μm ; caudal processes to 36 μm ; spine at base of toes to 23 μm .

Distribution: In Aufwuchs (i.e. periphyton attached to submergent stems). Two records only, Brisbane, Qld and from Creswick Ck, Clunes, Vic.

Literature: Thorpe 1887; Koste 1978; Berzins 1982.

Not recorded from Australia:

S. bifurca (Bolton, 1884) in Hudson & Gosse (1886) Europe, Iceland.

S. microductyla (Murray, 1906), Europe, Newfoundland, in *Sphagnum*.

Genus *Lepadella* Bory de St. Vincent

Lepadella Bory de St. Vincent, 1826, p. 86.

Outline oval, pear-shaped or circular, more or less dorso-ventrally flattened; dorsal and ventral lorica plates firmly joined; deep notch for head and foot; occipital margin of lorica often with granulated collar; head with cap-like plate. Dorsal lorica domed, smooth, with or without keel development, also with several ledges or fillers; lorica margins in some species drawn out into winglike extensions. Head and foot apertures of different shape; differences useful in taxonomy of group. Foot of three flexible segments, one inflexible basal segment. Toes short and pointed or long and needle-like, similar or dissimilar in length, inserted laterally or dorsal-ventrally, in some species completely or partly fused. Corona single ciliary wreath with lateral ciliary tufts and buccal field. Two lateral eye spots, occasionally with separate pigment granules

Fig. 3:1. *Squatinella rostrum* (Schmidta): (a) headshield, dorsal; (b) headshield, ventral; (c) dorsal; (d) lateral antenna, (e) ventral; (f) lateral. 2. *S. mutica* (Ehrenberg): (a) ventral; (b) lateral; (c) foot, lateral. 3. *S. longispinata* (Tatem): (a) lateral; (b) dorsal; (c) foot, lateral. 4. *S. leydigii longiseta* Pourriot. 5. *S. mutica tridentata* (Fresenius): (a) dorsal; (b) lateral. 1a, b, after Wehei (1898); 1c, 4, 2a, b, 4a, after Wulfert (1939); 2c–g, after Koste (1978); 3a, after Pejler (1962); 3b, after Stenroos (1898); 3c, after Myers (1942); 4b, after Gillard (1948); 5, after Pourriot (1971). Scale lines 50 μm .

nearby. Dorsal and lateral antennae present, latter generally dorsally situated at level of upper border of foot-opening. Last foot segment usually with caudal antenna. Trophi malleate, uncus with five teeth. Gut with large, sometimes lobed gastric glands. Vitellarium large with eight nuclei. Protonephridia with distinct terminal cells and large bladder. Little known of reproductive cycle. Some males (90–120 µm) are known. Resting eggs, with prickly outer shell, retained in lorica of parent on death.

Lepadella species are benthic, common in billabongs and ponds, but occasionally collected as incursion species in the plankton of reservoirs and rivers, e.g. *L. patella* (Shiel *et al.* 1982). Further details are given by Koste (1978), who notes that all species can be identified from preserved material, although caution must be taken with preservation artefacts, particularly in the case of formalin-preserved specimens. Several of the 45 taxa of *Lepadella* identified from Australia probably are misidentified for this reason. These are considered in the text. Nevertheless, about half of the known species appear to be indigenous; the genus is thus second only to *Brachionus* (Koste & Shiel 1987b) in its complement of endemic taxa.

Three subgenera are recognized on the basis of toe morphology:

- (i) *Lepadella* (toes of equal length, entirely separated);
- (ii) *Heterolepadella* (toes of unequal length);
- (iii) *Xenolepadella* (toes completely or partly fused).

For convenience, the Australian species of the three subgenera are considered separately in the following keys.

Key to species of the genus *Lepadella* (s. str.)

1. Dorsal lorica without keel or ribs (may be lightly punctate, but otherwise unornamented)..... 2
2. Dorsal lorica with keel and/or longitudinal ribs or other ornamentation..... 17
- 2(1). Lorica length >3x lorica width, almost cylindrical (Fig. 4:3)..... *L. angusta* Berzins
Lorica length <3x lorica width, ovoid, circular, trapezoidal or rhomboidal..... 3
- 3(2). Dorsal lorica cross-section 1/3 of circle to highly-domed hemisphere (Fig. 5:2d)..... 6
- 4(3). Lorica oval to circular; head aperture notched both dorsally and ventrally (Fig. 6:5a)..... *L. ovalis* (Müller)
Lorica 2x wider in posterior third than anterior; dorsal margin of head aperture straight, ventral margin only weakly V-shaped (Fig. 6:3b)..... 5
- 5(4). Ventral lorica with two lateral spines directed forward; toes straight (Fig. 9:2)..... *L. tana* Koste & Shiel
Ventral lorica spineless; toes curved..... *L. nehmssi* Berzins
- 6(3). Occipital margin of head aperture protruding (Fig. 5:8b)..... 10
Occipital margin of head aperture concavely notched (Fig. 5:4a)..... 7
- 7(6). Lorica outline elongate oval to circular (Fig. 5:7a)..... 8
Lorica outline rhomboidal (Fig. 5:4a)..... *L. chengaluthi* Koste
- 8(7). Posterior margin of lorica rounded or truncate, never pointed (Fig. 5:7a)..... 9
Posterior margin of lorica tapers to a pointed projection extending beyond base of toes (Fig. 9:7)..... *L. williamsi* Koste & Shiel
- 9(8). Head aperture ventral sinus with parallel cuticular ribs; dorsally with a wide granulated collar..... *L. elliptica* Wulff
Head aperture without ribs or dorsal collar..... *L. patella* (Müller)
- 10(6). Ventral lorica with longitudinal pleats..... *L. triba* Myers
Ventral lorica unpleated..... 11
- 11(10). Cross-section with rounded head-like lateral margins..... *L. daetyliseta* (Stentos)
Cross-section lateral margins produced to acute angled tips..... 12
- 12(11). Foot-opening excised dorsally..... 13
Foot-opening not excised dorsally..... 16
- 13(12). Extremely wide foot-opening, longer than wide; corners with outwardly-curved points..... 14
Foot opening wider than long, no points on corners..... *L. benjamini* Harring
- 14(13). Head aperture ventrally with lateral bifurcate pointed extensions extending beyond dorsal margin;..... *L. cornuta* (Koste)
No lateral points on head aperture;..... 15
- 15(14). Head aperture with convex dorsal margin; last foot segment <½ toe-length..... *L. latusinus* (Hilgendorf)
Head aperture with concave dorsal margin; last foot segment >½ toe-length..... *L. vitrea* Sheppard
- 16(12). Head aperture circular..... *L. apsida* Harring
Head aperture with deep ventral sinus..... *L. rottensburgi* (Lucks)
- 17(1). Lorica outline trapezoidal; lorica unornamented (apex) punctate or granulated under LP..... 18
Lorica outline circular or oval..... 19
- 18(17). Lateral extensions ("horns") from posterior lorica; rows of tiny rodlike structures cover lorica (Fig. 6:4a)..... *L. minor* Koste
Lateral horns absent; punctiform ornamentation of dorsal and ventral lorica (Fig. 9:5a)..... *L. tyleri* Koste & Shiel
- 19(17). Lorica outline circular; head aperture circular, ventrally placed; lorica cross-section an inverted saucer (Fig. 6:2)..... *L. lindutai* Koste
Lorica outline ovoid; head aperture not circular;

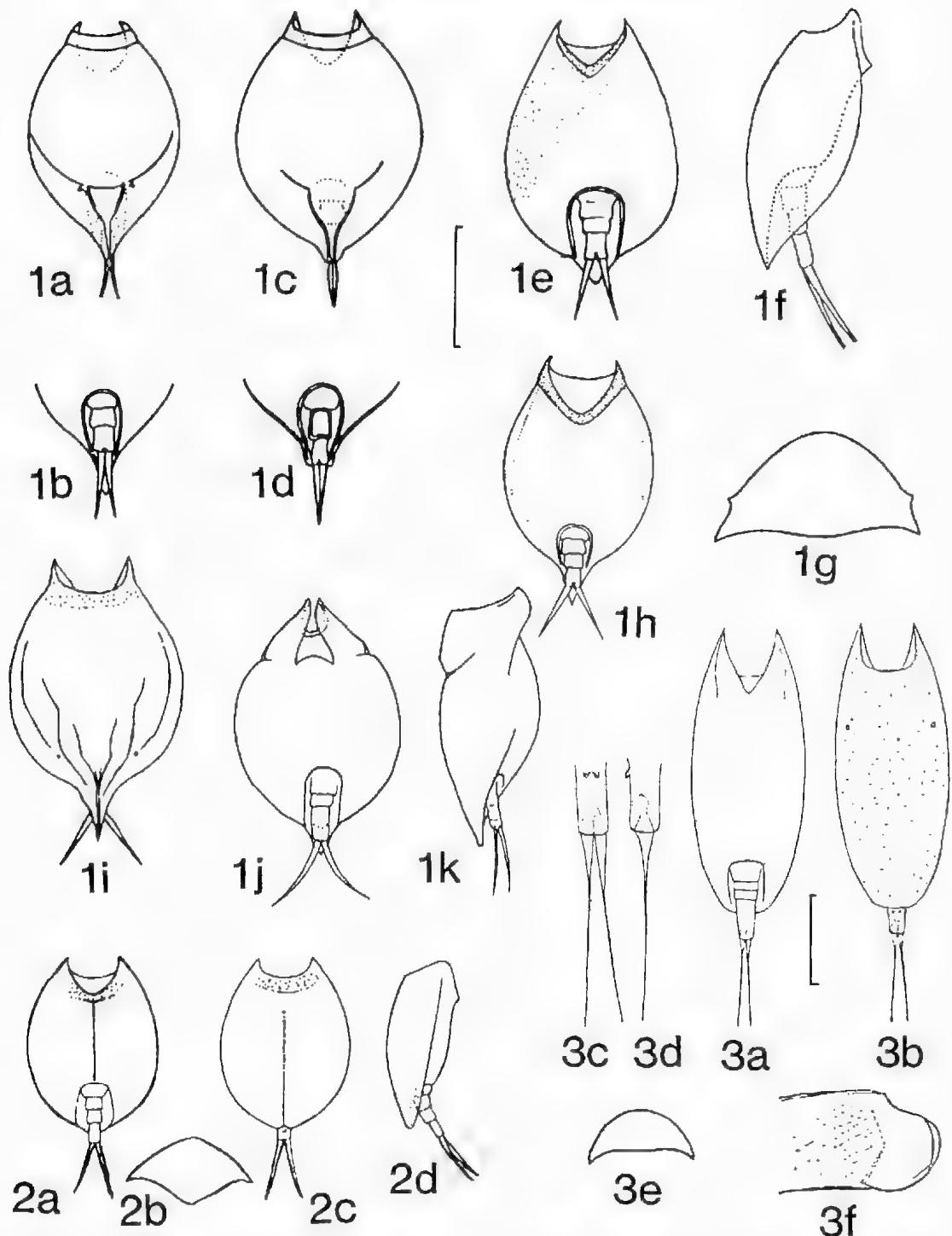


Fig. 4:1, *Lepadella acuminata* (Ehrenberg): (a) dorsal; (b) caudal morphology, ventral; (c) dorsal; (d) caudal morphology, ventral; (e) ventral; (f) lateral; (g) cross-section; (h) ventral; (i) *L. acuminata sexcostata*, dorsal; (j) *L. chorea*, ventral; (k) *L. chorea* lateral. 2, *L. amphitropis* Harring: (a) ventral; (b) cross-section; (c) dorsal; (d) lateral. 3, *L. angusta* Berzins: (a) ventral; (b) dorsal; (c) foot, distal segment, and toes, dorsal; (d) toes, lateral; (e) cross-section; (f) anterior, lateral. 1a-d, 1i, after Koole & Shiel (1980); 1a, f, g, i, k, after Berzins (1982); 2, after Harring (1916); 3, after Berzins (1960). Scale lines 50 µm.

- lorica cross-section lightly domed, ribbed or triangular 20
 20(19). Posterior lorica tapers to an acute point, which may be ridged dorsally
 *L. acuminata* (Ehrenberg)
 Posterior lorica rounded, indented, or concavely notched 21
 21(20). Dorsal lorica with median keel 24
 Dorsal lorica without median keel 22
 22(21). Dorsal lorica with open-squared pattern (three rows); occipital margin straight
 *L. decora* Berzins
 Dorsal lorica unpatterned, with 1–4 short ribs over foot-opening 23
 23(22). 1–3 short ribs at posterior end over foot-opening; cross-section rhombic
 *L. amphitropis* Hanning
 4 parallel short ribs over foot-opening; cross-section a shallow dome with lateral concavities of ventral margin (Fig. 8:2C)
 *L. quadricarinata* (Stenroos)
 24(21). Median keel of dorsal lorica without side ribs 25
 Median keel with 2–3 pairs of side ribs
 *L. quinquecostata* (Lucks)
 25(24). Median keel low and wide, bordered by lateral grooves; granulated collar
 *L. rhomboides* (Gosse)
 Median keel high, triangular, arising from narrow base; no granulated collar. Some forms have fine striped/pustulated lorica surface
 *L. triptera* (Ehrenberg)

N.B. Some European forms of *L. triptera* are noted by Koste (1978) to be rhomboidal. Only oval forms are known from Australia.

Lepadella acuminata (Ehrenberg)

FIG. 4:1

- Metopidia acuminata* Ehrenberg, 1834, p. 210.
Lepadella acuminata after Dujardin, 1841, p. 633.
Lepadella chorea Berzins, 1982, p. 18, Fig. 36

Diagnosis: Dorsal lorica with two lateral keels; caudal dorsal lorica variable, with small notch or strong elongated spikes, which may show short sharp or blunt ridge dorsally. Nominate sp. with points of dorsal lorica slightly offset laterally.

Length 64–110 µm; width 42–72 µm; toe length 18–35 µm.

Distribution: Cosmopolitan between water plants, in littoral of fresh standing and running waters, tolerates slight salinity increases, however prefers acid waters (Koste 1978). Uncommon; pancontinental, 10.0–29.8°C, pH 4.3–7.8, DO 6.1 mg l⁻¹, 28–1020 µS cm⁻¹, 8 NTU, Alk. 1.9 mg l⁻¹.

Comments: Several variant forms are known. On present evidence these are not considered of specific status. In *L. acuminata sexcostata* Bartos (Fig. 4:1) the dorsal lorica has six ribs, which run medially

to form an elongated ridge to the end of the lorica. *L. acuminata septemcostata* Berzins probably is an ecotypic variant. *L. chorea* Berzins (Fig. 4:1j, k) is inadequately figured, and appears to be a preservation artefact of *L. acuminata*.

Literature: Bartos 1955; Russell 1961; Koste 1978; Shiel & Koste 1979; Green 1981; Berzins 1982; Koste et al. 1983.

Lepadella amphitropis Hanning

FIG. 4:2

L. amphitropis Hanning, 1916, pl. 543

L. amphitropis victoriensis Berzins, 1982, p. 10, Fig. 25.

Diagnosis: Lorica cross-section rhombic due to curvature of the ventral lorica; lorica end with small notch; dorsal lorica end with one to three short ribs.

Length 69–76 µm; width 54–56 µm; height to 29 µm; toes 20–24 µm.

Distribution: In *Sphagnum*, middle Europe and Nth America. Rare; N.S.W., Tas., Vic. 9.5–17.0°C, pH 3.1–5.7, 80.6–98.3 µS cm⁻¹.

Literature: Hauer 1958; Koste 1962; Koste & Shiel 1987a.

Comment: A population from the Tarwin R., Vic. designated *Lepadella amphitropis victoriensis* by Berzins (1982) on the basis of the deep sinus on the ventral lorica does not differ in this feature from the nominate species. The measurements of the ssp. are, however, appreciably different: length 86 µm, width 60 µm, head-aperture 20 µm, dorsal sinus depth 8–12 µm, ventral sinus depth 14 µm; foot-opening 18–20×13–16 µm, toe length 15–18 µm. We retain subspecific status for this taxon until the extent of ecotypic variation can be determined.

Lepadella angusta Berzins

FIG. 4:3

L. angusta Berzins 1960, pp. 85–86, Figs 7–12.

Diagnosis: Lorica elongated, ventrally flat, dorsally convex; occipital margin with deep U-shaped dorsal sinus, deeper V-shaped ventral sinus; dorsal lorica sparsely punctate; dorsal pores unusually far forward, in anterior 1/3rd of dorsal lorica; foot groove broad, distally not reaching rounded posterior margin of lorica; foot long, with distal segment longer than two proximal segments combined; terminal segment with two small dorsal projections (Fig. 4:3c, d); toes long, thin, acute, wider proximally.

Length 115 µm (lorica 105 µm), width 46 µm, dorsal sinus 34×18 µm, ventral sinus 34×23 µm, foot groove 25×18 µm, foot and toes 65 µm (terminal segment 16 µm, toes 41 µm).

Distribution: Apparently endemic. Collected in

summer from the Plenty R., Morang, Vic. No other locality known. Ecology unknown. Superficially resembles *L. elliptica* (Fig. 5:7).

Lepadella apsida Harring
FIG. 5:1

L. apsida Harring 1916, p. 536, Fig. 89:1-3.

Diagnosis: Lorica almost circular; head aperture round, with posterior border drawn downward; toes very short.

Length 70 μm ; width 60 μm ; toes 12 μm .

Distribution: In riparian vegetation, N. America, Asia. Rare: billabongs (N.T.), I. Euramoo (crater lake) (Qld). 28.5°C, pH 5.4, DO 6.2 mg l⁻¹, 23 $\mu\text{S cm}^{-1}$.

Literature: Green 1981; Koste 1981.

Lepadella benjamini Harring
FIG. 5:2

L. benjamini Harring 1916, pp. 548-549, Fig. 93:1-8.

Diagnosis: Lorica outline broadly oval, head aperture more or less tubular, narrow, with ventrally-directed margins; lateral lorica margins in cross-section with bulging, beaded rim, or downturned; foot aperture wider than long; toes long, gently curved ventrally.

Length 112-114 μm ; width 85-100 μm ; height 44-52 μm ; head aperture 32-40 μm ; foot aperture 24x30 μm ; toes 45-48 μm .

Distribution: N. America, S. America (*L. brasiliensis* Koste 1972). Rare: I. Booti, Vic., N.T. billabongs. 20.0-24.5°C, pH 6.3-7.4, DO 5.1-8.8 mg l⁻¹, 42-1500 $\mu\text{S cm}^{-1}$.

Literature: Koste 1981.

Lepadella chengalathi Koste & Shiel
FIG. 5:4

L. chengalathi Koste & Shiel, 1980, p. 138, Figs 7 a-d.

Diagnosis: Rhomboidal lorica with rounded corners, widest in first third; head opening small, not deflected ventrally; foot-opening semicircular at widest point of caudal boundary of dorsal lorica; dorsal lorica weakly arched towards interior; three flexible foot-articulations, distalmost slender and elongated; toes symmetrical, long, needle-like, straight (Fig. 5:4b); lorica cross-section shows highly vaulted dorsal lorica with slender downward-drawn lateral wings; ventral plate with delicate double convex keel (Fig. 5:4d).

Length 135-140 μm (lorica 96 μm); width 92 μm ; height 48 μm ; head-opening width 28 μm ; foot-opening 28x28 μm ; distal foot segment 19-20 μm ; toes 33-36 μm .

Distribution: Endemic, only known locality L. Booti, Vic. 23.5°C, pH 7.9, DO 6.0 mg l⁻¹, 420 $\mu\text{S cm}^{-1}$, 67 NTU.

Lepadella cornuta nom. nov.
FIG. 5:3

Lepadella latusinus f. *mucronata* Koste, 1981, p. 119, Fig. 14a, b.

non *L. mucronata* Schmarda, 1859, p. 57, Pl. 13, Fig. 20, non *Metopidia mucronata* Dáday, 1908, p. 30.

Diagnosis: General posterior outline of lorica resembles *L. latusinus*, with extremely wide foot-opening; in *L. cornuta* opening wider in proportion to lorica width, i.e. body slightly more elongate; caudal margin lightly concave dorsally, ventrally with v-shaped sinus flanked by distinctive pointed lateral projections extending beyond dorsal margin; points are bifurcate in lateral view (Fig. 5:3 inset), with upper longer tips reflexed ventrally over shorter tooth.

Lorica length 110 μm ; width 62 μm ; foot-opening width 40 μm ; toe length 32 μm .

Distribution: Endemic, only record from Nakeen Billabong, Magela Creek, N.T. 29.9°C, pH 5.47, DO 5.45 mg l⁻¹, 44 $\mu\text{S cm}^{-1}$, alkal. 2.6 mg l⁻¹.

Lepadella dactylieta (Stenoos)
FIG. 5:5

Metopidia dactylieta Stenoos, 1898, p. 165, Fig. 3:1.
Lepadella dactylieta after Harring, 1916, p. 547, Figs 92:1-3.

Diagnosis: Caudal margin of dorsal lorica flat, even or convex; ventral margin with variable sinus (cf. *L. latusinus*); lorica cross-section always shows very pronounced dome; toes relatively short.

Length 93-100 μm ; width 60-66 μm ; height 40 μm ; toes 24-32 μm .

Distribution: Cosmopolitan in algal-rich standing waters, also lake littorals. Rare, Vic. 8.5-27.0°C, pH 7.0-7.6, DO 7.0-11.2 mg l⁻¹, to 575 $\mu\text{S cm}^{-1}$, 21-52 NTU.

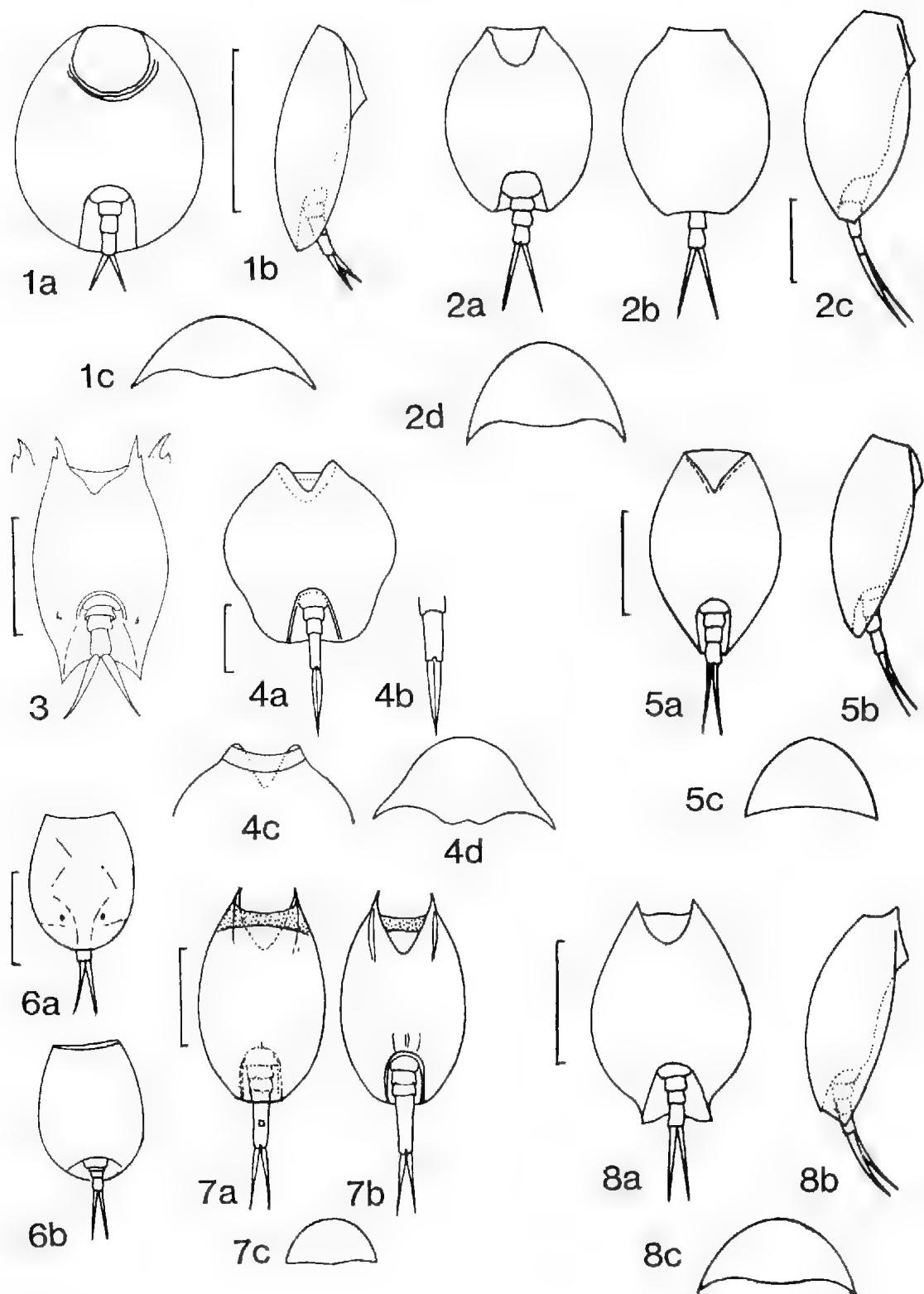
Literature: Koste & Shiel 1980; Berzins 1982.

Lepadella decora Berzins
FIG. 5:6

L. decora Berzins 1982, p. II, Figs 2a, b.

Diagnosis: Occipital margins nearly straight; dorsal lorica with open-squared pattern, arranged in three rows; robust pores on last third of dorsal lorica; ventral lorica slight; foot-opening wider than long, occupies whole posterior margin; toes straight, sharp.

Length 70 μm ; width 52-54 μm ; head-opening 35



μm ; foot-opening 12×30 – $32 \mu\text{m}$; toes 24–26 μm .

Distribution: Only known locality Loddon R., Victoria. Ecology unknown.

Literature: Berzins 1982.

Comment: Inadequately figured in Berzins (1982). We have reproduced Berzins figure, which does not show the patterning or pores described above. We have not encountered the species, however on the basis of the above description regard it as valid.

Lepadella elliptica Wulfert

FIG. 5:7

L. elliptica Wulfert 1939, p. 609, Fig. 21.

Diagnosis: Elongated lorica, hemispherical in cross-section (cf. *L. angusta*); head aperture with shallow U-shaped dorsal sinus, deep V-shaped ventral sinus, latter with accompanying parallel-bordered lateral cuticular pleats; distal foot-segment conspicuously long, tapering slightly to base of toes; toes relatively long, curved ventrally.

Length 108–115 μm ; width 70 μm ; distal foot-segment 28 μm ; toes 20–22 μm .

Distribution: Spotadic in littoral decomposition zone. Known only from a billabong of the Magela Ck, Jabiluka, N.T. 25.5°C , pH 6.2, DO 2.9 mg l $^{-1}$, 62 $\mu\text{S cm}^{-1}$.

Literature: Koste 1981.

Lepadella latusinus (Hilgendorf)

FIG. 5:8

Metopidia solidus latusinus Hilgendorf, 1899, p. 131, Fig. 11–15J.

Lepadella latusinus after Harring, 1913, p. 63.

Diagnosis: Lorica broadest in middle, tapers slightly to each end; cross-section vaulted hemisphere; occipital margin cowl-like, protruding; head aperture relatively small; extremely wide foot-opening, small spikes at margins hooked dorsally upwards.

Lorica length 80–92 μm ; width to 64 μm ; height 35 μm ; head aperture width 24 μm ; toes 24–28 μm . **Distribution:** In subtropical and tropical shallow waters (but recorded from Mt Cook, N.Z.), warm stenotherm. Rare: N.I. 24.0 – 27.0°C , pH 4.5–6.3, DO 5.1 mg l $^{-1}$, 42 $\mu\text{S cm}^{-1}$.

Comment: A variant described by Koste (1981) from Nankeen Billabong, N.T. as *L. latusinus* cf. *visenda* (Fig. 6:1a) had features of *L. latusinus* and *L.*

visenda Myers (Fig. 6:1b). Only one individual was encountered, insufficient material for further analysis.

Literature: Myers 1934; Russell 1945; Koste 1978.

Lepadella lindaui Koste

FIG. 6:2

L. lindaui Koste 1981, pp. 109–110, Fig. 2.

Diagnosis: Wide egg-shaped lorica, occasionally with almost-circular outline; head aperture ventral, nearly circular, at times bordered around lower part by cuticular ribs; foot opening parabolic to elliptical; caudal margin rounded or lightly indented. Lorica flat. Dorsal lorica in cross section slightly arched with wide raised hump, which in posterior third, accompanied by two converging pleats, carries flat keel, terminating in fine point reaching caudal margin. Lateral antennae papillae small on end of oblique lorica fold (Fig. 6:2a). Sensory pit present on distal foot segment.

Lorica length 80 μm ; width 68 μm ; head aperture 22 μm ; lorica height 20 μm ; foot aperture 23 μm ; toes 12 μm .

Distribution: Only known localities. Mombasa, Kenya and Winimurra billabong, Magela Creek near Jabiluka, N.T. 28.5°C , pH 5.4, DO 6.2 mg l $^{-1}$, 22 $\mu\text{S cm}^{-1}$, alkal. 2.7 mg l $^{-1}$.

Lepadella minoru Koste

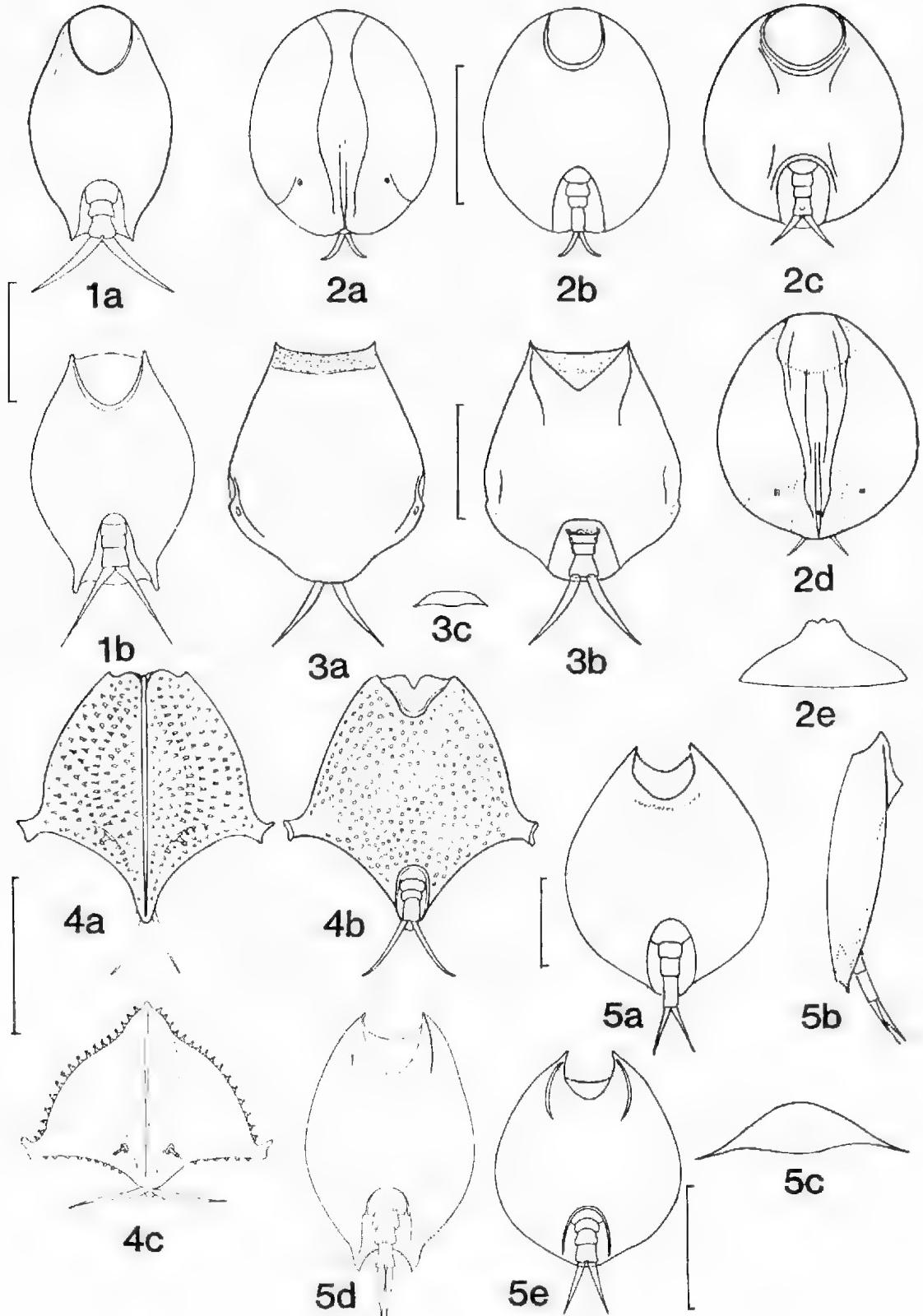
FIG. 6:4

L. minoru Koste, 1981, pp. 110–113, Fig. 3.

Diagnosis: Lorica outline in upper part trapezoidal with wings (ductlike; terminally concave (Fig. 6:4a, b)); lorica tapers symmetrically from wings, ending in pointed protrusion covering foot-opening; head aperture (ventral) smoothly indented, dorsally with median notch; thin keel runs from notch to posterior lorica margin; ventral plate flat, with robust bead-like structures (unpatterned); dorsal lorica covered with 3–6 μm long rods in rows parallel to margins outside, and with keel on inner rows. Rods sit on circular bases. Lateral antennae dorsal, located approximately level with anterior margin of foot-opening, with pistill-like papillae; foot 3-segmented; toes lightly curved ventrally, pointed.

Lorica length 72–80 μm ; width 76–80 μm ; height 48 μm ; toe length 24 μm ; head aperture width 24 μm , depth 12 μm ; foot-opening width 16 μm .

Fig. 5:1, *Lepadella apicula* Harring: (a) ventral; (b) lateral; (c) cross-section. 2, *L. benjamini* Harring: (a) ventral; (b) dorsal; (c) lateral; (d) cross-section. 3, *L. curvata* (Koste), ventral. 4, *L. chengalathii* Koste & Shiel: (a) ventral; (b) distal segment of foot and toes; (c) occipital margin, dorsal; (e) cross-section. 5, *L. thalassica* (Stenroos): (a) ventral; (b) lateral; (c) cross-section. 6, *L. decora* Berzins: (a) dorsal; (b) ventral. 7, *L. elliptica* Wulfert: (a) dorsal (b) ventral; (c) cross-section. 8, *L. latusinus* (Hilgendorf): (a) ventral; (b) lateral; (c) cross-section. 1, 2, 5, 8, after Harring (1916); 3, after Koste (1981); 4, after Koste & Shiel (1980); 6, after Berzins (1982); 7, after Wulfert (1939). Scale lines 50 μm .



Distribution: Endemic, Leichhardt and Wimmera billabongs. Magela Creek near Jabiluka, N.T. 28.5–30.1°C, pH 5.4–5.5, DO 5.5–6.3 mg l⁻¹, 23–58 µS cm⁻¹, alkal. 2.7–2.9 mg l⁻¹.

Lepadella neboissi Berzins
FIG. 6:3

L. neboissi Berzins 1960, p. 53, Figs 1–3.

Diagnosis: Outline of body broadly ovate; greatest width slightly posterior to middle of body; lorica strongly dorso-ventrally flattened, without ridges; anterior dorsal margin straight, ventral margin with wide V-shaped sinus and short fold present on each side; lorica rounded posteriorly. Sinus and fold slightly behind the middle of body, on each side of lorica, with corresponding pores on dorsal side; foot groove nearly as long as wide; foot rather short, terminal segment longer than first and second segments combined; toes relatively long, divergent, pointed at apex.

Total length 105–108 µm (lorica 78–81 µm); width of anterior lorica 63–66 µm; ventral sinus 11–13 µm deep; foot groove 18–19x12 µm; foot 14–16 µm; toes 30 µm.

Distribution: Endemic, King Parrot Creek, near Kinglake West, Vic.

Comment: Resembles *L. monodi* Berzins from Senegal, Africa, but differs in the form of the lateral sinus and the pores for lateral antennae on the margin.

Lepadella ovalis (Müller)
FIG. 6:5

Brachionus ovalis Müller, 1786, p. 345, Fig. 49:1–3.

Lepadella ovalis after Ehrenberg, 1830; p. 45, Fig. 7:4 non *Metapidia ovalis* Anderson & Sheppard, 1892, p. 78 (see *L. vitrea*).

Diagnosis: Lorica outline oval to circular; wide space between internal organs and lorica margins; ventral lorica nearly flat; lorica at rim thinly tapered; narrow striated area at outer margin from head aperture to foot-opening; outline of foot-opening variable; gastric glands often lobed and long-stalked. Juvenile animals sometimes have caudal notch dorsally over foot-opening. Males known. Resting egg shell covered with robust, lightly curved spines.

Lorica length 90–170 µm; width 70–140 µm;

height 25–30 µm; toe length 22–36 µm; foot opening to 48 µm deep, 32 µm wide.

Distribution: Cosmopolitan, between macrophytes in benthos of fresh and saline waters. Uncommon; pancontinental. Ecotypes described from Australian waters include a form from the Magela Creek, N.T. (Fig. 6:5d) and a minute form from L. Dulverton, Tas (Fig. 6:5e). 8.2–24.0°C, pH 5.8–7.7, 273–3330 µS cm⁻¹.

Literature: Koste 1978, 1981; Shiel & Koste 1985; Koste & Shiel 1986a.

Lepadella patella (Müller)
FIG. 7:1

Brachionas patella Müller, 1786, p. 341, Fig. 48:15–19.
Lepadella patella after Bory de St Vincent, 1826, p. 86.

Diagnosis: Lorica outline ovoid to circular; dorsal lorica domed, without wings; ventral lorica flat, occasionally with somewhat overhanging margins; wide lorica forms more domed in cross-section than narrower forms (Wulfert (1960) described flat and domed forms from *Sphagnum*); variable foot opening (Hauer (1962) found caudal corners of foot-opening extended into spines, while one specimen described by Wulfert *loc. cit.* had almost circular foot-opening); occasionally, dorsal lorica adjacent to foot-opening has weakly distinguishable folds. Male known.

Length 120–145 µm; lorica length 70–110 µm; width 65–90 µm; length:width ratio mostly <1.2; toe length 20–35 µm; male 110–120 µm.

Distribution: Cosmopolitan, eurytopic in fresh and saline waters. Common; pancontinental. Ecotypic variants are known from N.T. (Fig. 7:1e) and Tas. (Fig. 7:1g), 10.0–24.5°C, pH 3.9–8.8, DO 7.8–11.6 mg l⁻¹, 9.2–6600 µS cm⁻¹, 3.0–262 NTU.

Literature: Koste 1978, 1981; Shiel & Koste 1985.

Comment: Several recognized subspecific variants of *L. patella* are recorded from Australian waters. The status of these taxa may change with detailed systematic work.

Lepadella patella biloba Hauer
FIG. 7:2

Lepadella patella biloba Hauer, 1958, pp. 27–28, Fig. 2:14.
L. patella f. *biloba* (Hauer) by Koste, 1978, p. 185.

Diagnosis: Lorica outline resembles *L. patella*, however differs from f. typ. in three features: lateral corners of foot-opening reflexed dorsally (Fig. 7:2d);

Fig. 6:1, (a) *Lepadella latiusinus* cf. *visenda*, ventral; (b) *L. visenda* Myers, ventral; 2, *L. lindauai* Koste; (a) N.I. form, dorsal; (b) ventral; (c) Mombasa form, ventral; (d) dorsal; (e) cross-section. 3, *L. neboissi* Berzins: (a) dorsal; (b) ventral; (c) cross-section. 4, *L. minoris* Koste: (a) dorsal; (b) ventral; (c) cross-section. 5, *L. ovalis* (Müller): (a) ventral, (b) lateral; (c) cross-section. 6, N.T. form; (e) Tas. form la, 2, 4, 5d, after Koste (1981); 1b, after Myers (1934); 3, after Berzins (1960); 5a-c, after Harring (1916); 5e, after Shiel & Koste (1985). Scale lines 50 µm.

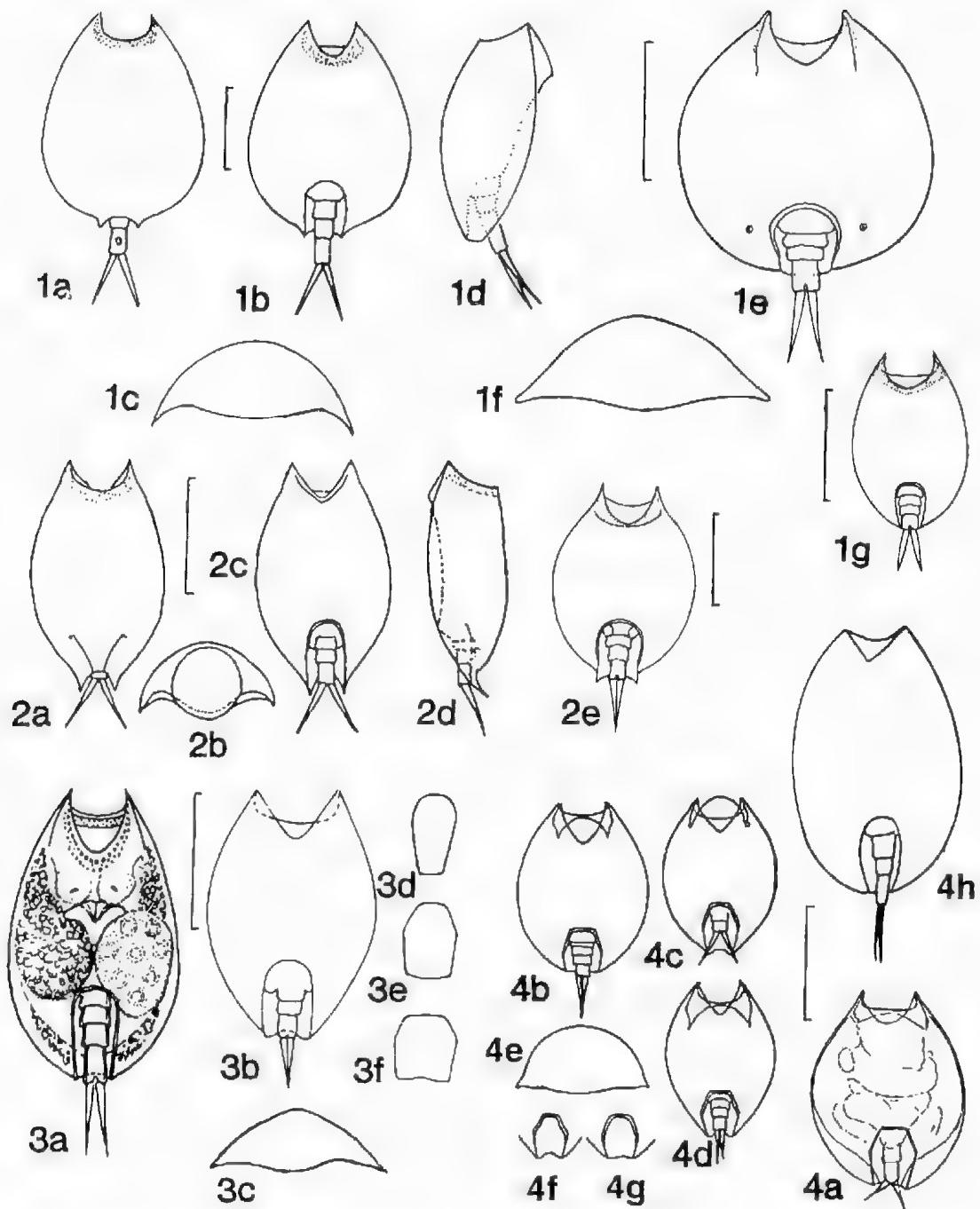


Fig. 7:1. *Lepadella patella* (Müller): (a) dorsal; (b) ventral; (c) lateral; (d) cross-section; (e) N.I. form, ventral; (f) cross-section; (g) Tas. form, ventral. 2, *L. patella hiloba* Hauer: (a) dorsal; (b) cross-section; (c) ventral; (d) lateral; (e) Tas. form, ventral. 3, *L. patella oblonga* Ehrenberg: (a) ventral; (b) ventral; (c) cross-section; (d-f) variations in foot-opening morphology. 4, *L. patella similis* (Lucks): (a) ventral; (b-d) different lorica forms, ventral; (e) cross section; (f-g) foot-opening, ventral; (h) *L. huangensis* Berzins, ventral. 1a-d, after Harring (1916); 1e, f, after Koste & Shiel (1980); 1g, 2e, after Koste & Shiel (1986); 2a-d, 4b-g, after Hauer (1958); 3a, c, after Wulfert (1939); 3b, d-f, after Björklund (1972); 4h, after Berzins (1982). Scale lines 50 μm .

ventral lorica with lateral concavities, side margins deflected downwards (Fig. 7:2b); two short cuticular folds of caudal dorsal lorica.

Length 80–107 µm; width 59–64 µm; height 36 µm; toes 19–25 µm.

Distribution: Europe. Rare! Tas., Vic., southwest W.A. 11.8–24.0°C, pH 3.5–7.9, 18.3–2130 µS cm⁻¹. **Literature:** Koste et al. 1983; Shiel & Koste 1985.

Lepadella patella oblonga (Ehrenberg)

FIG. 7:3

Squaniula oblonga Ehrenberg, 1834, p. 220.

Lepadella oblonga (Ehrenberg) after Harring, 1913, p. 64. *Lepadella patella* s. *noblonga* after Wulfert, 1960, p. 285, Fig. 24.

Diagnosis: Distinguished from *L. patella* only by relatively low lorica height and narrow head aperture. Lorica outline mostly elliptical,

Lorica length 80–110 µm; width 50–70 µm; length:width ratio >1.5; toes 20–25 µm.

Distribution: In fresh and brackish water pools, often sympatric with the nominate species and *L. patella similis*. Björklund (1972) demonstrated biometrically distinguishable populations, however intergrades with *L. patella* typ. occur;

Only Australian record from Sheepwash Billabong, near Yea, Vic., 17.iv.76 (Shiel unpubl.), 19.9°C, pH 7.2, DO 8.5 mg l⁻¹, 85 µS cm⁻¹, Secchi transparency 80 cm.

Literature: Koste 1978

Lepadella patella similis (Lucks)

FIG. 7:4

Metopidia similis Lucks, 1912, p. 119, Fig. 39.

Lepadella similis (Lucks) after Häuer, 1925, p. 17

L. patella var. *similis* after Remane, 1929, p. Fig. 113A–F.

L. buangensis Berzins, 1982, p. 11, Fig. 5.

Diagnosis: Lorica outline elliptical; foot-opening with reinforced upper arch (Fig. 7:4 f, g), mostly hexagonal with angled edges and base straight to indented. Not reliable taxonomic character because of variability in foot-opening. Distinguished from *L. patella* (s. str.) by lorica length:width ratio (>1.2) and overall smaller habit.

Length 68–85 µm; width 49–60 µm; toes 17–21 µm.

Distribution: Between macrophytes, detritus, in sandstone and rock pools; fresh, brackish and salt; pH to 10 (Koste 1978). Single record from Australia (as *L. buangensis* Berzins), but recognizable as a preservation artefact of *L. patella similis*, Mt Donna Buang, Vic.

Lepadella ptilota Berzins

FIG. 8:1

L. ptilota Berzins, 1960, pp. 83–85, Figs 4–6.

Diagnosis: Body ovoid in outline; ventral surface slightly medially convex, dorsal surface very strongly so; dorsal median line with sharp, uneven longitudinal ridge; frontal margin dorsally convex, with blunt projection in the middle; ventrally with rounded sinus; laterally, lorica enlarged with three pairs of thin, transparent lamellar projections; lorica prolonged posteriorly to rounded lobe; cross section somewhat triangular.

Length 72–75 µm; width 60–67 µm; ventral sinus depth 8 µm; length of foot groove 12–15 µm; toes 12 µm.

Distribution: Endemic. Only known locality Creswick Creek near Clunes, Victoria. Ecology unknown.

Comment: Resembles *L. triplex* (Ehrenberg) but differs in the form of the frontal margin of the lorica, the sharp dorsal ridge, and the presence of lateral cuticular projections (termed "flappers" in the original description although they have no muscular contact).

Lepadella quadricarinata (Steenoos)

FIG. 8:2

Melopidia quadricarinata Steenoos, 1898, p. 165, Fig. 3:2.

Diagnosis: Dorsal lorica with four short ribs over foot-opening; posterior end tapering to short tongue; ventral lorica flat; foot opening variable.

Lorica length 81–92 µm; width 61–72 µm; height to 34 µm; toe length 20–26 µm.

Distribution: Littoral, between macrophytes, pH 6.2–10.2 (Koste 1978). Only record that of Berzins (1982) from Coghill's Creek near Tourello, Vic. *L. q. sexcarinata* (Klement), recorded from the same locality, may be an ecotype.

Literature: Koste 1978.

Lepadella quinquecostata (Lucks)

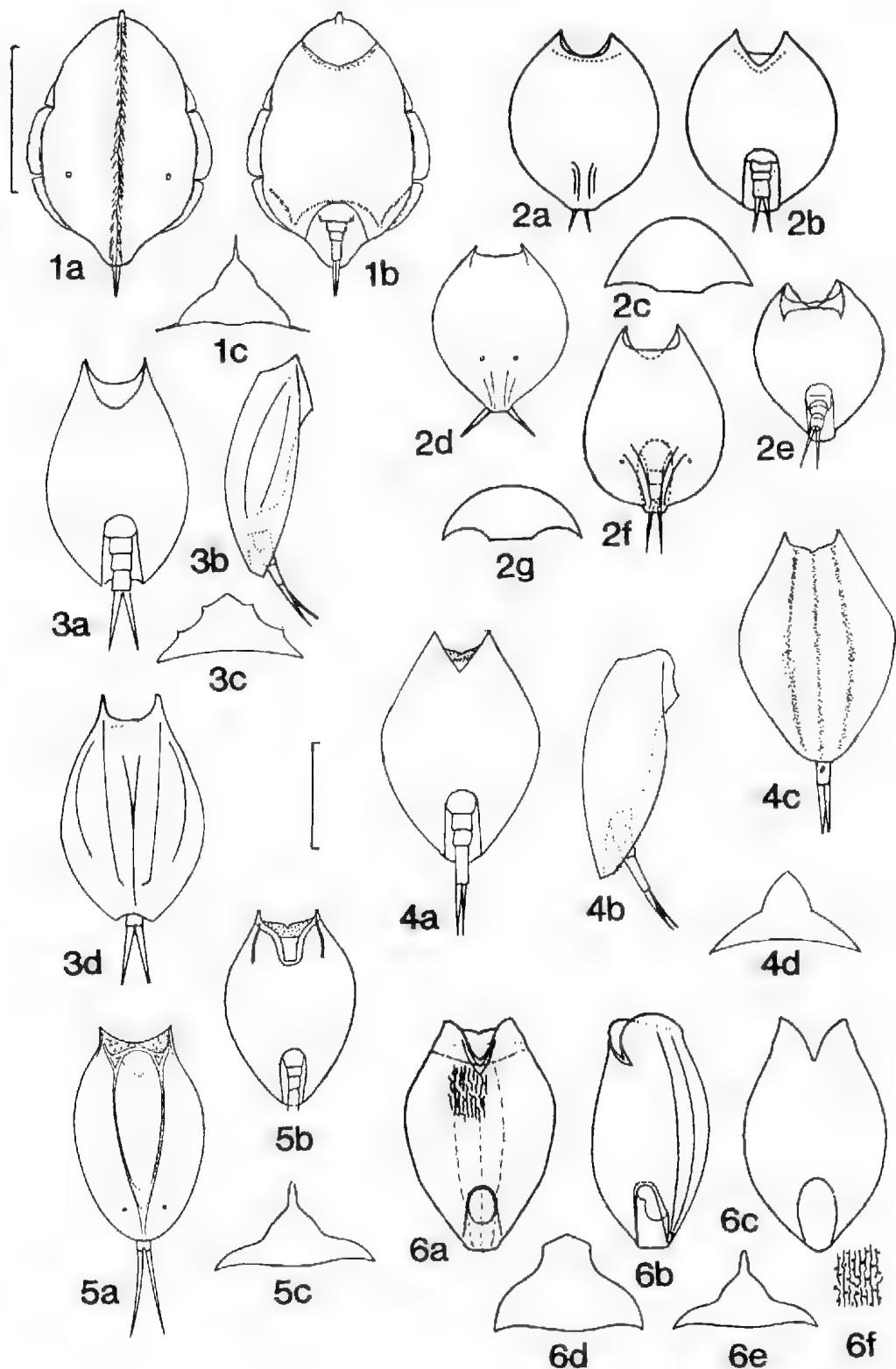
FIG. 8:3

Melopidia quinquecostata Lucks, 1912, p. 126, Fig. 47.

Diagnosis: Lorica pyriform, narrowing towards head; dorsal lorica with median low keel which begins as widely separated ridges behind collar of head aperture; two or three pairs of side ribs; distinctive cross-section (Fig. 8:3c); lorica end variable, sometimes with short ridge; foot-opening variable.

Lorica length 92–112 µm; width 60–70 µm; toe length 22–30 µm.

Distribution: Cosmopolitan in littoral, often



collected in *Sphagnum*, pH 4.5–6.7, temperature to 30°C (Koste 1978). Single record: dam near Chillagoe, Qld.

Lepadella rhomboides (Gosse)
FIG. 8:4

Metopidia rhomboides Gosse in Hudson & Gosse, 1886, p. 108, Fig. 25:10.
Lepadella rhomboides after Harring, 1913, p. 65.

Diagnosis: Dorsal lorica with moderately high, more or less arched median keel, bounded by lateral grooves; anterior margin width $\frac{1}{4}$ lorica length; dorsal sinus broadly U-shaped; ventral sinus V-shaped; dorsal aperture of head-opening with collar, which can be bordered by cuticular thickening; foot opening narrow, U-shaped with parallel sides; distal foot segment long (cf. *L. elliptica*); toes short ($<\frac{1}{4}$ body length) slightly decurved, tapering to points.

Lorica length 110–120 µm; width 55–88 µm; toe length 20–28 µm.

Distribution: Cosmopolitan in periphyton, pH tolerant. Rare: N.S.W., N.T., Tas., Vic. 10.5–30.7°C, pH 4.7–7.9, DO 4.6–6.0 mg l⁻¹, 23–750 µS cm⁻¹, to 67 NTU, alkal. 2.7–2.9 mg l⁻¹.

Comment: Two variants are known from Australia, described elsewhere as spp., form or var.: *L. rhomboides haueri* (Wulffert) (Fig. 8:5) from a stock dam south of Burnie, Tas. (16.5°C, pH 4.7, 42 µS cm⁻¹) and *L. rhomboides carinata* (Donner) (Fig. 8:6) from the Broken R. at Benalla, Vic. (27.0°C, pH 7.6, DO 7.0 mg l⁻¹, 52 µS cm⁻¹).

Literature: Kutikova 1970; Koste 1978; Koste et al. 1983; Koste & Shiel 1986a.

Lepadella rotenburgi (Lucks)
FIG. 9:1

Metopidia rotenburgi Lucks, 1912, p. 127, Fig. 48a, b.
L. rotenburgi after Harring, 1913, p. 65.

Diagnosis: Side margins of lorica cross-section extend to pointed tips below level of median ventral bulge; head aperture dorso-ventrally deep, only ventral sinus; dorsal margin straight, without sinus; foot-opening variable. Resembles *L. dactylieta*. Can be confused with *Colurella* spp. in lateral view.

Lorica length 75 µm; width 50 µm; toes 25–28 µm.
Distribution: Isolated occurrences in *Sphagnum* and

peat swamps. Only record Riddell's Creek, Sunbury, Vic.

Literature: Koste 1978; Berzins 1982.

Lepadella tana Koste & Shiel
FIG. 9:2

Lepadella tana Koste & Shiel, 1987, p. 102, Fig. 19.

Diagnosis: Lorica broadly ovoid, ventral lorica flat, dorsal medially convex in median cross-section; dorsal margin of head-opening almost straight, ventral margin with weak V-shaped sinus; fold behind middle of body on ventral surface; with pointed, slightly curved spine on either side, directed apically; foot-opening broad; toes relatively long, straight, sharply pointed.

Lorica length 79 µm; width (medially) 61 µm; anterior width 29 µm; foot-opening 18x18 µm; toes 29 µm; lateral spine length 18 µm.

Distribution: Endemic; only known locality L. Pedder, Tasmania, 16.5°C, pH 5.3, 46.2 µS cm⁻¹.

Comment: Resembles *L. neboissi*, a Victorian endemic (Fig. 6:3), however the latter has ventral folds (no spines), and differs in foot- and toe morphology.

Lepadella tripla Myers
FIG. 9:3

Lepadella tripla Myers, 1934, pp. 4–5, Figs 10–12.

Diagnosis: Lorica elongated; cross-section shallow, evenly arched dorsally; dorsal margin of head aperture almost straight, ventrally broadly V-shaped; no stippled collar; ventral lorica with distinctive *Euchlanis*-like slightly elevated mid-section (Fig. 9:3c), lateral margins run to head aperture or diverge to side apices; foot opening flaring; distal foot segment approximately $\frac{1}{2}$ toe-length; toes long, tapering to slender drawn-out tips.

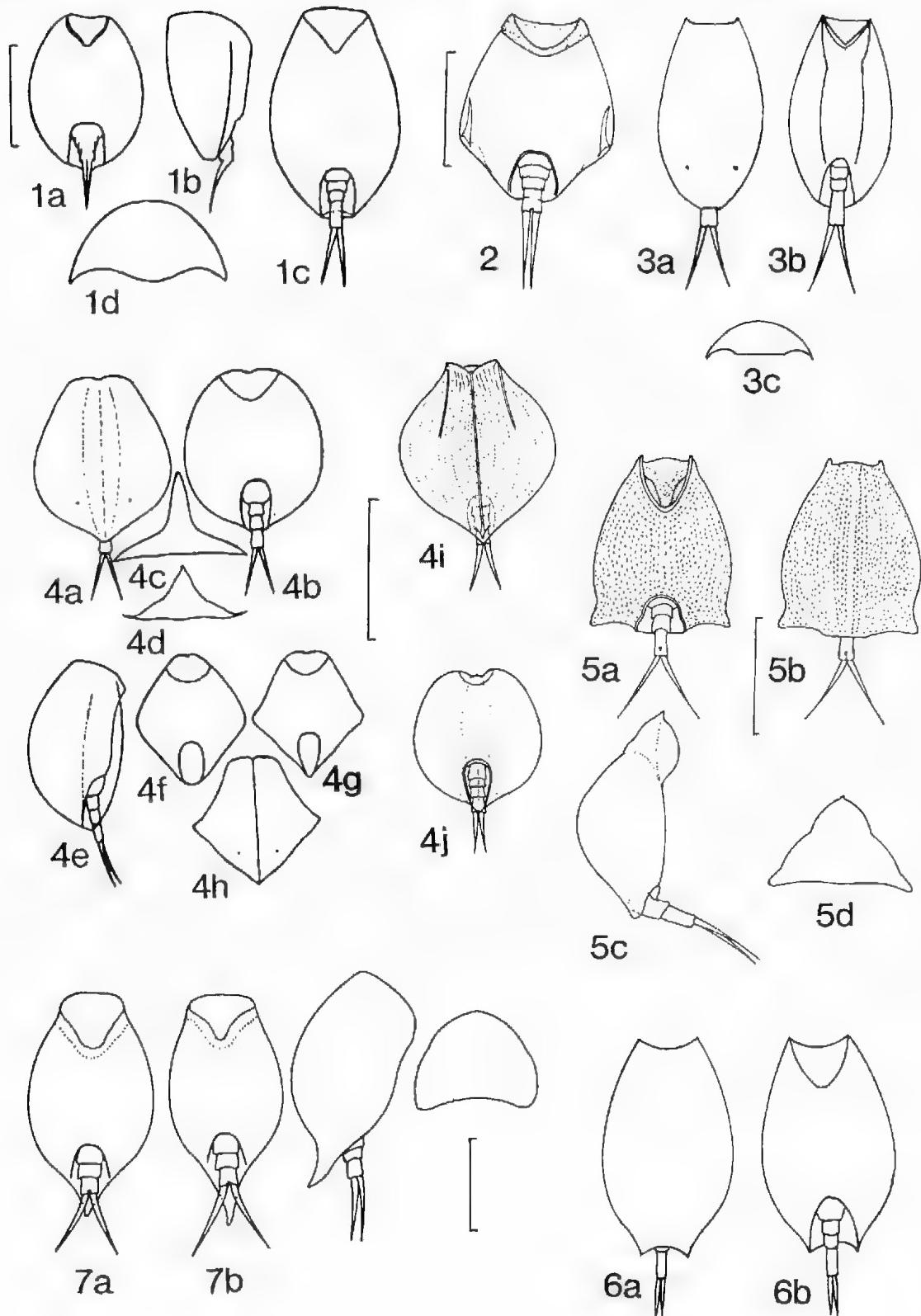
Lorica length 71–80 µm; width 42–45 µm; ventral sinus depth 12 µm; foot opening depth 20 µm; foot length 26 µm; distal segment 14 µm; toes 30–33 µm.

Distribution: North America. Single record from Qld (Berzins 1982) needs verification.

Lepadella triptera (Ehrenberg)
FIG. 9:4

Metopidia triptera Ehrenberg, 1830, pp. 74–83.
Lepadella triptera Ehrenberg, 1832, p. 72.

Fig. 8:1, *Lepadella pilota* Berzins: (a) dorsal; (b) ventral; (c) cross section. 2, *L. quadricarinata* (Stentoros): (a) dorsal; (b) ventral; (c) cross-section; (d) dorsal; (e) ventral; (f) dorsal; (g) cross-section. 3, *L. quinquecostata* (Lucks): (a) ventral; (b) lateral; (c) cross-section; (d) dorsal. 4, *L. rhomboides* (Gosse): (a) ventral; (b) lateral; (c) dorsal; (d) cross section. 5, *L. rhomboides haueri* (Wulffert): (a) N.T. form, dorsal; (b) European form, ventral; (c) cross-section. 6, *L. rhomboides carinata* (Donner): (a) ventral; (b) lateral; (c) ventral; (d) cross section spec. a'; (e) cross-section spec. c'; (f) lorica surface morphology. 1, after Berzins (1980); 2a–c, 1, 5b, e, after Bartov (1959); 2d, g, after Pejler (1962); 2e, after Björklund (1972); 3, 4, after Harring (1916); 5, after Koste (1981); 6, after Donner (1943). Scale lines 50 µm.



Diagnosis: Lorica outline variable; circular to rhombic according to Koste (1978). Dorsal lorica vaulted, with high, somewhat protruding median keel; head aperture with shallow U-shaped sinus ventrally, usually slight median notch dorsally; lorica surface may be finely striped (Fig. 9:4) with small rounded protusions, most, however, are smooth.

Lorica length 58–65 µm; width 50–57 µm, toes 13–22 µm.

Distribution: Cosmopolitan in fresh and brackish waters, and on muddy littorals. Rare: N.S.W., N.T., Qld., Tas., Vic. 12.4–20.0°C, pH 4.8–7.7, 17–330 µS cm⁻¹.

Literature: Shiel & Koste 1979; Koste 1981; Herzins 1982.

Lepadella tyleri Koste & Shiel

FIG. 9:5

Lepadella tyleri Koste & Shiel, 1987a, p. 37, Figs 3, 4.

Diagnosis: Rigid lorica of trapezoidal outline; cross-section nearly triangular; dorsal plate with median keel; dorsal and ventral plates finely granulated; head aperture lightly convex dorsally, deep V-shaped sinus ventrally, with lateral lamella; caudal lorica with slight constriction above blunt lateral corners; foot-opening broadly flared; three foot segments, distal with caudal antenna; toes very thin, elongated, pointed.

Total length 123–125 µm; lorica length 78–80 µm; greatest width 58 µm; height 36 µm; head aperture width 21 µm, depth 22 µm; foot opening 18x18 µm; distal foot segment 12 µm; toes 32 µm.

Distribution: Endemic; only known locality a stock dam south of Swansea, east coast of Tasmania, 13.0°C, pH 6.0, 390 µS cm⁻¹, 82 NTU.

Lepadella vitrea (Shephard)

FIG. 9:6

Metopidia ovata Shephard in Anderson & Shephard, 1892, p. 78, Fig. 6, 6a, 1106 *M. ovata* (Müller, 1786).

M. vitrea Shephard, 1911, p. 55.

Lepadella vitrea after Hanning, 1913, p. 65.

Diagnosis: Ovoid, transparent lorica, tapering to each end from widest part posterior to midline; head aperture slightly convex dorsally, without

sinus, ventrally with deep, broadly elliptical sinus; dorsal margin of foot opening convex between lateral points of slightly downturned caudal lorica projections; ventral foot opening deep ½-ellipse; distal foot segment almost twice length of proximal segments, more than half length of toes; toes short, tapering to pointed tips.

Length 125 µm; width 56 µm. [No other measurements given in the original description, however from Fig. 6 in Anderson & Shephard (1892), on the basis of their length/width measurements, the following are estimated: head aperture 23 µm wide x 20 µm deep; foot opening 20 µm wide x 22 µm deep; distal toe joint 12 µm; toes 17 µm.]

Distribution: Subsequent to the original find (Brighton, Victoria), *L. vitrea* was recorded from South Westland, N.Z. (Russell 1954). Dimensions were slightly different (114 µm long, toes 20 µm), with "a series of dots round the lateral edge of the dorsal plate"; *L. vitrea* is possibly more widespread.

Comment: *L. vitrea* was synonymised with *L. latiusculus* by later reviewers (e.g. Koste 1978), however can be distinguished from the latter by more elongated lorica (length:width ratio 2.2 vs <1.5 in *L. latiusculus*), absence of cowl-like head aperture, elongated distal foot segment and markedly shorter toes.

Lepadella williamsi Koste & Shiel

FIG. 9:7

Lepadella williamsi Koste & Shiel, 1980, pp. 138–139, Fig. 8.

Diagnosis: Smoothly oval, highly vaulted lorica, with ventrally-directed head-opening; dorsal lorica tapers caudally to variable-length laterally curved point; foot-opening narrow, ending at base of dorsal lorica projection; three foot segments of similar length; long, dorso-laterally curved sharp toes.

Lorica length 112–116 µm; width 60–64 µm; height to 56 µm; head aperture 33–36x28–30 µm; caudal lorica projections 19–28 µm; foot opening 17–20x19–20 µm; distal foot segment 10 µm; toe length 36–40 µm.

Distribution: Kuala Lumpur, Malaysia, and Jabi Iuka, N.T. only known localities. 25.5°C, pH 6.2, DO 2.9 mg l⁻¹, 62 µS cm⁻¹, 5 NTU.

Fig. 9:1, *Lepadella rottenburgi* (Lucks); (a) ventral; (b) lateral; (c) ventral; (d) cross-section 2, *L. tana* Koste & Shiel, ventral; 3, *L. tribu* Myers (a) dorsal; (b) ventral; (c) cross-section; 4, *L. triptera* (Flürenberg); (a) dorsal; (b) ventral; (c) cross-section; (d) cross-section; (e) lateral; (f–h) different lorica forms, ventral; (i) Tas. form, ventral; (j) 2nd Tas. form, ventral; 5, *L. tyleri* Koste & Shiel; (a) ventral; (b) dorsal; (c) lateral; (d) cross-section; 6, *L. vitrea* (Shephard); (a) dorsal; (b) ventral; 7, *L. williamsi* Koste & Shiel; (a, b) two morphs, ventral; (c) lateral; (d) cross-section. 1a, b, after Caling (1939); 4c, d, after Bartos (1959); 2, 4i, j, after Koste & Shiel (1986); 3, after Myers (1934); 4a, b, after Hanning (1916); 5, after Koste & Shiel (1987a); 6a, orig.; 6b, after Shephard (1911); 7, after Koste & Shiel (1980). Scale lines 50 µm.

**Key to species of the genus *Lepadella*
(*Heterolepadella*)**

- 1. Lorica oval 2
- Lorica rhomboidal 3
- 2(1). Head aperture with V-shaped dorsal and ventral sinuses *L. (H.) heterodactyla* Fadeev
Head aperture with only a ventral sinus, dorsal margin straight *L. (H.) upsicora* Myers
- 3(1). Lorica with posterolateral pointed spurs; foot groove with lateral pointed projections
..... *L. (H.) ehrenbergi* (Perry)
Lateral wings of lorica and posterior margins of foot groove rounded *L. (H.) heterostyla* Murray

Lepadella (Heterolepadella) upsicora Myers
FIG. 10:1

Lepadella apricota Myers, 1934, pp. 5, 7, Figs 16–18.

Diagnosis: Lorica oval; cross section shallow, evenly arched dorsally; dorsal anterior margin nearly straight, ventral margin with deep V-shaped sinus; stippled collar present; foot groove wide, flared posteriorly; distal foot joint 2x length of combined first and second joints; foot twisted, left toe lies beneath right; toes asymmetric, right 2x length of left.

Lorica length 80 µm; width 65 µm; ventral sinus depth 18 µm; anterior points 28 µm; foot groove 21 µm; foot 30 µm; distal segment 20 µm; right toe 30 µm; left 14 µm.

Distribution: North America. Two records from Australia: L. Boort, central Victoria, and Wimurra Billabong, Magela Creek, N.T. 23.5°C, pH 5.4–7.9, DO 6.0–6.2 mg l⁻¹, 23–750 µS cm⁻¹, 67 NTU, alkal. 2.7 mg l⁻¹.

Literature: Koste & Shiel 1980; Koste 1981.

L. (H.) ehrenbergi (Perry)
FIG. 10:2

Notuxonia ehrenbergi Perry, 1850, p. 20.

Metopidia ehrenbergi after Jennings, 1894, p. 26.

Lepadella ehrenbergi after Herring, 1913, p. 63.

Diagnosis: Lorica rhombic, with posterolateral margins produced to triangular, dorsally ridged spurs reflexed upwards in cross-section (Fig. 10:2c); smaller pointed spurs on each side of foot groove; stippled collar on ventral plate, with less obvious dorsal stippling; foot groove ¼ length of lorica, rounded anteriorly, flaring slightly posteriorly; foot stout, ½ length of lorica; distal foot joint longest; toes long, asymmetric, taper evenly.

Lorica length 70–95 µm; width 70–90 µm; toe length 27–32 µm and 19–27 µm.

Distribution: Cosmopolitan in periphyton, *Ulrichia*

laria and moss. Rare; in billabongs and vegetated lake margins in N.S.W., N.T., Qld., Vic. 24.0–29.2°C, pH 6.3–7.5; DO 5.1–8.0 mg l⁻¹, 42–85 µS cm⁻¹, 6 NTU.

Literature: Shiel & Koste 1979; Koste & Shiel 1980; Green 1981; Koste 1981.

L. (H.) heterodactyla Fadeev
FIG. 10:3

L. (H.) heterodactyla Fadeev, 1925, p. 73, Pl. 1, Fig. 8.

Diagnosis: Lorica oval; dorsal and ventral margins of head aperture with deep, almost triangular sinuses; last foot segment longer than preceding segments.

Lorica length 106–113 µm; width 70–75 µm; distal foot segment 22–23 µm; toes 23–30 and 20–25 µm.

Distribution: Europe, S. America (Amazonia). Single record, L. Boort, central Vic. 20.0 °C, pH 7.4, DO 8.0 mg l⁻¹.

Literature: Kutikova 1970; Koste 1978; Koste & Shiel 1980.

L. (H.) heterostyla (Murray)
FIG. 10:4

Metopidia heterostyla Murray, 1913, p. 459, Pl. 19, Fig. 6a–c.

Diagnosis: Lorica rhombic; lateral wings rounded rather than pointed (cf. *L. ehrenbergi*), with tips more or less deflected dorsally; ventral lorica wider than dorsal in region of head aperture; stippled collar present.

Distribution: Probably cosmopolitan in littoral zones, stagnant waters. Rare: N.S.W., Tas., Vic. 10.0–23.5°C, pH 5.8–7.9, DO 6.0–9.8 mg l⁻¹, 80–750 µS cm⁻¹, 2–67 NTU.

Literature: Koste 1978; Shiel & Koste 1979; Koste & Shiel 1980.

Not recorded from Australia:

L. (H.) cyrtopus (Harring). Eastern Europe, N. and Central America.

A single free-living species of the subgenus *Lepadella (Xenolepadella)* is recorded from Australia. In view of the preferred habitat of most of the other known species of the genus, i.e. the branchial chambers of a range of crustaceans, it is likely that other species occur here but have been overlooked.

Lepadella (Xenolepadella) monodactyla Berzins
FIG. 10:5

Lepadella monodactyla Berzins, 1960, pp. 5, 6, Figs 8–11.

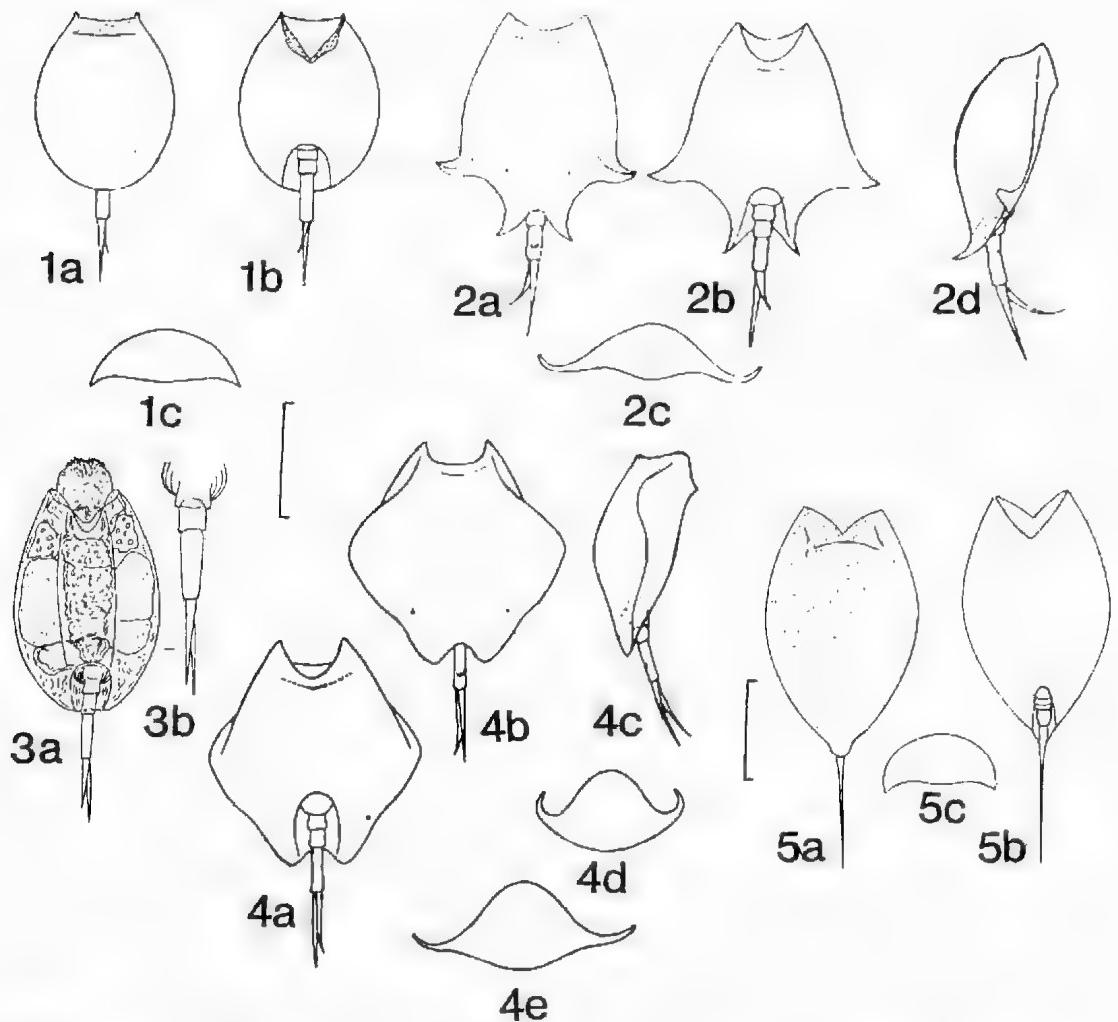


Fig. 10:1, *Heterolepadella apsicura* Myers: (a) dorsal; (b) ventral; (c) cross-section; 2, *H. chrenbergi* (Perty): (a) dorsal; (b) ventral; (c) cross-section; (d) lateral. 3, *H. heterodactyla* Fadeev: (a) ventral; (b) dorsal; (c) lateral; (d, e) different cross-sections; 4, *H. heterostyla* Murray: (a) ventral; (b) dorsal; (c) cross-section; 5, *Xenolepidella monodactyla* Berzins: (a) dorsal; (b) ventral; (c) cross-section. 1, 2, after Harring (1916); 3, after Kutikova (1970); 4, after Harring (1916); 5, after Berzins (1960). Scale-lines 50 μm .

Diagnosis: Lorica outline elliptical; dorsal lorica arched, punctate or lined; ventral plate with light bulge medially, otherwise unstructured; head aperture with V-shaped dorsal and ventral sinuses.

Total length 170 μm ; lorica length 127 μm ; width 77 μm ; foot-opening 31x10 μm ; toe 57 μm .

Distribution: Madagascar, variants known from Brazil. Single record, billabong, Jabiluka, N.T. 25.5°C, pH 6.2, DO 2.9 mg l⁻¹, 62 $\mu\text{S cm}^{-1}$.

Literature: Koste 1978; Koste & Shiel 1980.

Not recorded from Australia:

L. (X.) astacicola Harring, *L. (X.) borealis* Harring, *L. (X.) branchicola* Hauer, *L. (X.) haueri*

Rodewald, *L. (X.) lata* Wisniewski, *L. (X.) parasitica* Hauer, *L. (X.) pygmaea* (Gosse). See Koste 1978:198–200 for details).

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PRELIMINARY INVESTIGATIONS OF BEACH RIDGE PROGRADATION ON EYRE PENINSULA AND KANGAROO ISLAND

BY A. D. SHORT, R. C. BUCKLEY**, & D. G. FOTHERINGHAM†*

Summary

Field investigations along 2150 kin of the South Australian coast including the Great Australian Bight, Eyre Peninsula and Kangaroo Island revealed numerous sites with low wave energy beach ridge and occasional chenier plains. Examination of 14 mainland sites and six sites on Kangaroo Island indicate that all ridges are wash deposited during episodic wave events, probably over a period of decades to centuries. The ridges overly intertidal shelly sandflats. The oldest innermost tidal flats date at 6.3 ka and 5.9 ka BP, but the oldest ridge dated at 4 ka BP suggests a period of tidal flat formation and progradation is required before a source of sediment and plat form for ridge formation is available. All ridges and ridge sequences dated between 4 and 2 ka BP with no ridges material younger than 1.8 ka BP. While this confirms a delayed start for ridge development it does not necessarily imply no present ridge building as reworked, older shells may be incorporated in the modern ridges. The age and elevation of the sites lend support to a published sea-level curve for northern Spencer Gulf. The limited evidence available suggests that sea-level reached its present level in the Bight by 6 ka BP with no conclusive evidence for changes since.

KEY WORDS: Beach ridges, sea-level, Eyre Peninsula, Kangaroo Island.

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Field investigations along 2150 km of the South Australian coast including the Great Australian Bight, Eyre Peninsula and Kangaroo Island revealed numerous sites with low wave energy beach ridge and occasional chenier plains. Examination of 14 mainland sites and six sites on Kangaroo Island indicate that all ridges are wash deposited during episodic wave events, probably over a period of decades to centuries. The ridges overly intertidal shelly sandflats. The oldest innermost tidal flats date at 6.3 ka and 2.9 ka BP, but the oldest ridge dated at 4 ka BP suggests a period of tidal flat formation and progradation is required before a source of sediment and platform for ridge formation is available. All ridges and ridge sequences dated between 4 and 2 ka BP with no ridges material younger than 1.8 ka BP. While this confirms a delayed start for ridge development it does not necessarily imply no present ridge building as reworked, older shells may be incorporated in the modern ridges. The age and elevation of the sites lend support to a published sea-level curve for northern Spencer Gulf. The limited evidence available suggests that sea-level reached its present level in the Bight by 6 ka BP with no conclusive evidence for changes since.

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Introduction

The South Australian coast, west of Whyalla and including Kangaroo Island and the 78 islands of the Eyre Peninsula, represents 60% of the state's coastline. The coast contains a variety of Holocene shoreline types ranging from tide dominated sandflats to, with increasing wave energy, cheniers, beach ridges and regressive (foredune ridges) and transgressive barrier-dune systems (Short 1988a). The latter include some of Australia's most extensive coastal dune systems, including more than 500 km of cliff-top dunes (Short 1988b).

Whilst the 3700 km S. Aust. coast possesses a wide range of Holocene coastal depositional systems, the nature and evolution of these systems received only cursory attention until this decade. Regional studies and detailed investigation have only just begun to address the status of the coast. In the gulf regions Holocene sedimentation and Pleistocene and Holocene sea-level history associated with beach ridge plains have been investigated by Burne (1982), Belpério *et al.* (1983), Hails & Gostin (1984) and Belpério *et al.* (1988). Hails & Gostin (1984) and colleagues also presented a series of papers on the evolution of northern Spencer Gulf and its implications for modern sedimentation. In St Vincent Gulf, Bowman & Harvey (1986) conducted extensive coring and

dating of the La Pevre Peninsula to reconstruct the evolution of this important beach-ridge complex.

On the open coast three recent regional studies of the South East, Kangaroo Island and Eyre Peninsula (Short & Hesp 1984; Short & Fotheringham 1986; Short *et al.* 1986) provide the first comprehensive assessment of the morpho dynamics and Holocene evolution of these sections of coastline. The aim of this paper is to assess the evolution of the low wave energy beach ridge and chenier sites on Kangaroo Island and Eyre and their implications for mid to late Holocene sea-level in the region. Beach ridges are here defined as shore linear, low sandy-shelly swash deposits, separated by wider inter- and supra-tidal sand flats. They are a product of periodic wave action and should not be confused with aeolian foredune ridges, which have also been called beach ridges (see Hesp 1984). Cheniers have similar ridges but are underlain and separated by finer sediments such as muds, slits or fine muddy sands.

Beach ridges occupy only 4% (66 km) of Eyre Peninsula and (6%) 30 km of Kangaroo Island. This is not surprising given the generally high wave energy together with high percentage of rocky coast (66 and 64% respectively). On Eyre Peninsula beach ridges are common in the central gulf and occur in several protected bays on the Bight coast, while on Kangaroo Island they are restricted to the protected north eastern coves (see Short *et al.* 1986 and Short & Fotheringham 1986 for location of all sites). These sites are, however, very important for the interpretation of both Holocene shoreline evolution and sea-level history particularly given

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the noise or absence (due to erosion) of the more dominant higher-energy beach and dune deposits. Both Burne (1982) and Belperio *et al.* (1983, 1988) use such deposits to interpret Holocene sea-level history, particularly in northern Spencer Gulf, while Burne (1982) and Bowman & Harvey (1986) identified episodes of ridge-building in northern Spencer and St Vincent gulls, respectively. This paper provides a preliminary assessment of the initiation and timing of ridge-building at 20 sites together with some implications for mid to late Holocene sea-level in these regions.

Study Area

All beach ridge-chenier sites were identified by mapping the entire coastal geomorphology using 1:10,000 colour aerial photography. Twenty representative sites were selected for field investigations (Fig. 1). They represent about 50% of both regions beach ridge systems. Table 1 lists environmental parameters of each site.

Field investigations involved surveying of cross ridge transects using a theodolite; and both surface and shallow (<1 m) subsurface sampling, the latter using both shovel and hand auger. All samples were collected within 10 cm stratigraphic units usually from *in situ* tidal flat deposits. All shells were collected within each layer. For dating only the most intact valve or bivalve shells were collected assuming that the more intact and fresh the appearance, the less distance they have been transported and therefore the younger they might be, thereby providing a more accurate minimum age of the deposit. Unless otherwise indicated, dated shells were obtained from the base of the anger-shovel hole. The location of each sample is illustrated in the accompanying figures.

All sites are characterised by low breaker wave conditions, with essentially zero modal ocean wave effects. Wave energy is delivered both by greatly attenuated (<1 m) extreme ocean waves and, more frequently, by local wind waves (<1 m). Tides range from micro (<1 m) on the open coast to 2.5 m on the mid Spencer Gulf (Fig. 1). Orientation to the dominant west to south-west winds and sea breezes is important only in relation to wind wave generation, since the beach ridges sites have little or no aeolian capping.

Results

Spencer Gulf

The five Spencer Gulf sites are listed in Table 1 and illustrated in Fig. 2. Tidal range increases from 1 m at Tukka Well to 2.5 m at Glensea. Glensea and Tukka Well receive periodic low wind waves, while

Point Germein, The Knob and particularly Lipson Cove receive more regular southerly wind waves.

Glensea' Beach Ridges

The eight swash deposited beach ridges (site 1, Fig. 1; Fig. 2) near Glensea Homestead are part of an extensive beach ridge plain which runs 110 km from just south of Whyalla to Lucky Bay. The ridges are fronted by extensive intertidal sandflats totalling 100 km². Many of the ridges, such as those at Glensea, interdigitate with partially submerged Quaternary longitudinal dunes, with the dunes forming low 'headlands' and ridges occupying the intervening 'embayments'. Dating of five of the ridges (Fig. 3a and Table 2) suggests ridge development commenced after 2.6 ka BP. The mixture of ages in ridges 6, 7 and 8 suggests that the outer ridges may be contaminated by older shells. If so, their age may be younger than indicated. During this time their carbonate content increased from 2 to 30–60% indicating dependence on biogenic production for sediment supply. The surface slope of the ridges and particularly the swales (Fig. 3a) could be attributed either to a fall in sea-level of 1.0 m during this period, or a reduction in incident wave energy because of sandflat development. Examination of the subsurface morphostratigraphy will be required to assess the causes.

Point Germein Beach — Foredune Ridges

Point Germein (site 2, Fig. 1) is part of the 13 km long Windmill beach-barrier that has prograded northward, thus partially blocking Franklin Harbour, and subsequently seaward. The age of the innermost beach ridge at the transect location only indicates the arrival of the northward prograding barrier there at 3220 ± 80 yr BP (Fig. 3b; Table 2). Subsequently, the barrier has prograded 250 m eastward into the Gulf with increasing aeolian capping producing a 5 m high foredune at the present shoreline. The elevations of the three inner beach ridges are all within the limit of present day swash action and also suggest rapid shoreline progradation compared to the higher outer ridges (4–8, Fig. 3b).

The Knob — Shingle Ridges

The 11 exposed shingle ridges at The Knob (site 3, Fig. 1; Fig. 3c) record storm wave deposition of coarse Tertiary conglomerate material. Whilst no dates were obtained, the seaward decrease in ridge elevation could be attributed to a relative fall in sea-level of ~1 m. However the evidence is inconclusive without subsurface stratigraphy and dates; all ridge

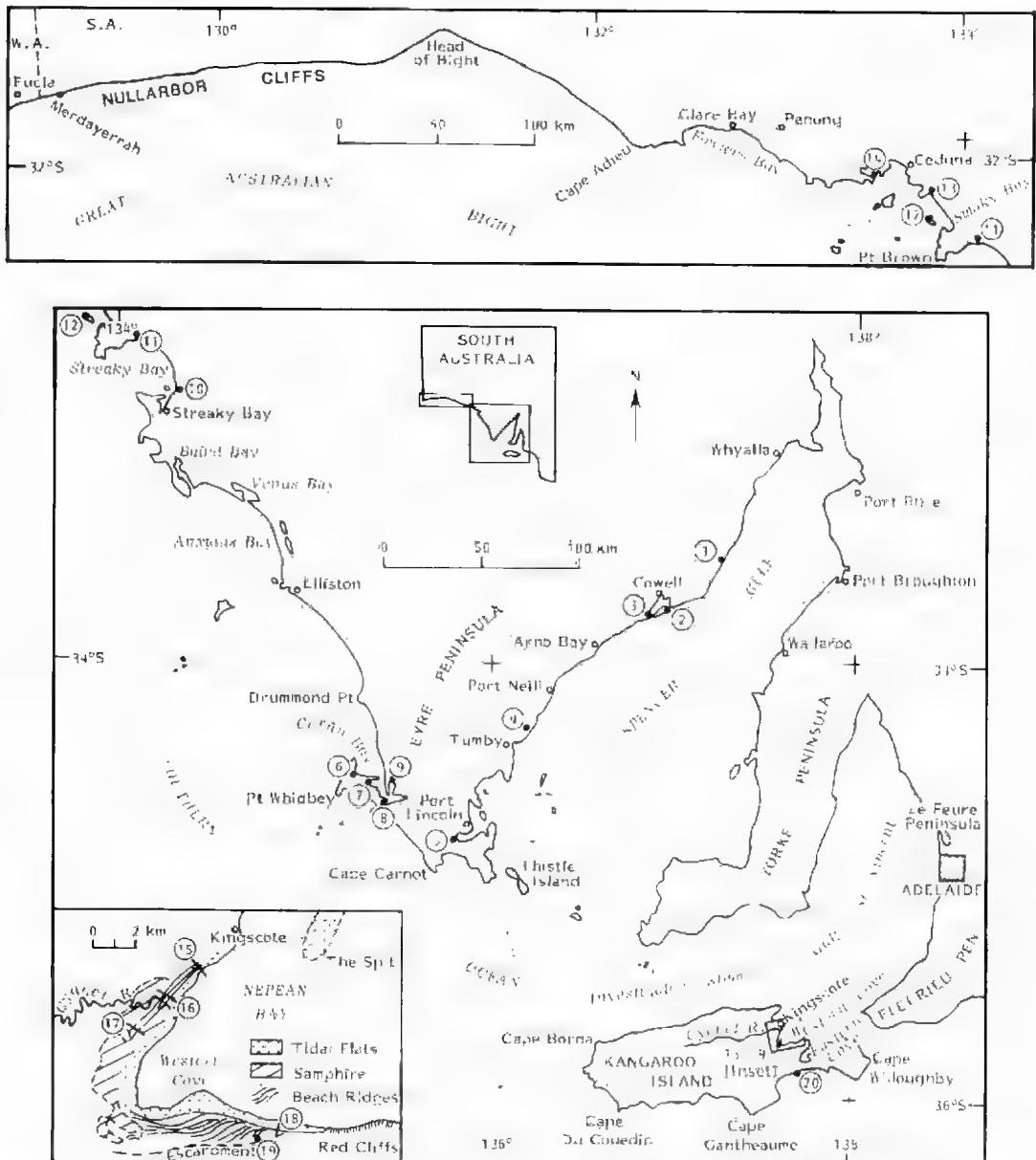


Fig. 1. Location map showing portion of the South Australian coast and location of the 20 sites (1–20) discussed in text. See Table 1 for names of sites. Lower insert is of Western Cove (sites 15–19) on Kangaroo Island.

crests are also within the reach of contemporary storm swash. Following progradation the ridges were buried by dune transgression, and later exhumed as a deflation surface, suggesting that shingle ridge formation preceded the deposition of barrier sands, corresponding to the finding of Burne (1982) in northern Spencer Gulf.

Lipson Cove Shingle Ridge

Shingle ridges back many of the sandy beaches along the western Spencer Gulf, particularly in the vicinity of the Tertiary conglomerates. At Lipson Cove (site 4, Fig. 1) a single shingle ridge (Fig. 3d) has been emplaced landward of the present beach,

Table 1. Site Location^a and characteristics

Location	Distance ^b	Morphology	Marine Energy
WEST SPENCER GULF:			
1. 'Glensea'	1579 km	8 beach ridges	southerly wind waves
2. Point Germein	1628	7 beach foredune ridges	southerly wind waves
3. The Knob	1633	11 shingle ridges	southerly wind waves
4. Lipson Cove	1721	1 shingle ridge	southerly wind waves
5. Tulka Well	1856	low beach ridges	northwesterly wind waves
GREAT AUSTRALIAN BIGHT:			
a. Coffin Bay			
6. Morgan's Landing	2089	4 beach ridges	occas. swell and N. wind waves
7. Salt Waterhole	2114	7 foredune ridges	relief; previously low swell
8. Yangie Bay	2133	tidal flats	no waves
9. Mount Dutton Bay	2172	3 beach ridges	low S wind waves only
b. Western Eyre Peninsula			
10. Perlubie Beach (S)	2544	beach-foredune ridges	W wind waves
11. Aeraman Creek	2583	multiple beach-ridges - spits	W & S wind waves; occas. swell
12. Eyre Island	2635	multiple beach-ridges - spits	occas. swell & W wind waves
13. Laura Bay	2683	6 beach ridges	occas. swell & S wind waves
14. Tourville Bay	2766	3 cheniers and mangroves	occas. swell
KANGAROO ISLAND:			
15. Brownlow	26 km	5 beach ridges	N & E wind waves
16. Brownlow (golf course)	38	7 beach ridges	N & E wind waves
17. Cygnet River	31	2 chenier beach ridges	N & E wind waves
18. Morrison Beach	42	tidal flat	N & E wind waves
19. Morrison Beach	43	back barrier depression	N & E wind waves
20. Pennington Bay	156	shore platform	open swell

^aMainland distance based on CSIRO Australian Coastal Inventory kms 0 km at SA/Vic border with km increasing to west to 3277 km at SA/WA border (Galloway *et al.* 1984).

^bDistance on Kangaroo Island based on clockwise measurement from North Cape (Short & Fotheringham 1986).

The location of the ridge suggests deposition prior to sandy beach formation, while its crest elevation of 4 m above ISLW is within the reach of contemporary storm waves.

Tulka Well — Beach Ridges

Tulka Well (site 5, Fig. 1) is a protected low wave energy site receiving only wind waves generated across Port Lincoln proper by north-east winds. The small, isolated beach ridge plain consists of several low ridges which have prograded approximately 150 m into the bay. Dates obtained from three holes dug in lee of the innermost ridge indicate that this was tidal flat by at least 3510 ± 80 yr BP (sample CS 531 Table 2, Fig. 3e). The dates (WK 837 and CS 531) indicate upward accretion of 25 cm over 0.6 ka, a rate of 0.04 mm yr⁻¹. Following the upward accretion of the tidal flats, some time subsequent to 2.5 ka BP, the low ridges prograded across the flats 150 m into the bay. The inner samphire — tidal flat tidal flat limit could be interpreted as lying up to 40 cm above the present tidal flat limit suggesting

a slight fall in sea-level. While De Deckker *et al.* (1982) also invoked a progressive fall in sea-level over the last 5–6 ka to explain decreased salinity in nearby Pillie Lake, the present data were inconclusive.

The Great Australian Bight (Western Eyre Peninsula)

The Great Australian Bight (the Bight) is exposed to some of the world's highest and most persistent waves (Chelton *et al.* 1980). However shelf attenuation (Provis & Steedman 1985), coast orientation and the presence of extensive nearshore calcarenite substantially reduces wave energy at many sites, even on the open coast (Short *et al.* 1986). As a result low energy beach ridges and cheniers are found in a number of locations particularly in the larger bays — Coffin, Venus, Baird, Streaky, Smoky, Decres and Tourville (Fig. 1). Nine sites were investigated. They are located in Coffin (4), Streaky (2), Smoky (1), Decres (1) and Tourville (1) bays, (Table 1, Figs 1, 4).

Coffin Bay

Morgan's Landing.

Morgan's Landing (site 6, Fig. 1) contains four beach ridges backed by a back barrier depression dominated by a *Melaleuca* swamp (Fig. 4a). In addition, shell-rich beachrock is exposed on the beach in front of the ridges (Table 3). Three dates were obtained. The oldest (WK 829), from the back-barrier swamp, dates at 3690 ± 190 yr BP, with the rear of the innermost ridge dating at 2540 ± 60 yr BP (WK 827) and shell in the beach calcarenite at 2680 ± 80 yr BP (CS 527). This suggests that progradation of the three ridges occurred around 3–2.5 ka BP and that since then the shoreline has been relatively stable. This stability is interrupted by west to east moving pulses of sand (sandwaves) that alternately prograde (such as when beach calcarenite was deposited) and erode the beach (such as at present) as they pass.

Salt Waterhole.

A 1 km wide series of at least seven low foredune ridges has prograded north-eastward of the Salt Waterhole (site 7, Fig. 1; Fig. 4b). The ridges apparently prograded at a time when a tidal channel existed between the Waterhole and the present Point Longnose. The eastward growth of Point Longnose subsequently closed the channel and terminated ridge progradation. Three dates were obtained from

the back barrier depression and the swash deposited base of the first (oldest) and fourth ridge. The back-barrier sample (WK 829) dated at 3440 ± 60 yr BP, the inner ridge (WK 830) at 3930 ± 60 yr BP, and the fourth ridge (CS 528) at 3190 ± 80 yr BP. These dates suggest a period of ridge progradation beginning about 4.0 Ka and continuing to some time beyond 3.2 ka BP, probably around 3.0 ka BP. At this time it is likely the channel was closed by the eastward growth of Point Longnose causing the ridges to be cut off from periodic ocean wave attack and sediment sources.

Yangie Bay.

Yangie Bay (site 8, Fig. 1, Fig. 4c) is a subsidiary embayment in the southern part of Coffin Bay. It is a zero wave energy environment where Holocene sedimentation is dominated by tidal and biogenic activity. One date (CS 529) was obtained from tidal flats surrounding an outcrop of Pleistocene dune calcarenite and should indicate the commencement of tidal flat progradation in this part of the bay. It dated at 2780 ± 80 yr BP (Fig. 4d). The other date (WK 832) was taken at 60 cm depth beneath samphire flats extending from the calcarenite and dated at 2080 ± 60 yr BP. Both dates suggest that substantial tidal flat progradation did not commence until around 3.0 ka BP. Stratigraphic examination of the site (Fig. 4d) also suggests that there has been little if any change in sea-level since that date.

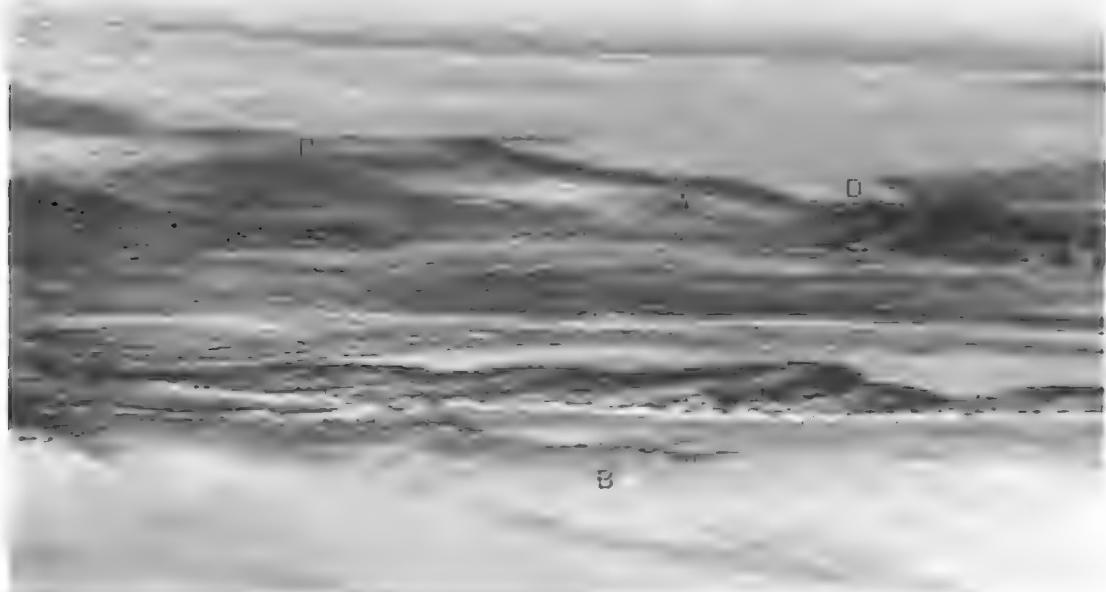


Fig. 2. The beach ridge plain near Glensea is located amongst longitudinal Pleistocene dunes (D). The transect (Fig. 3) extends from A across the ridges to B on the inner intertidal sand flats.

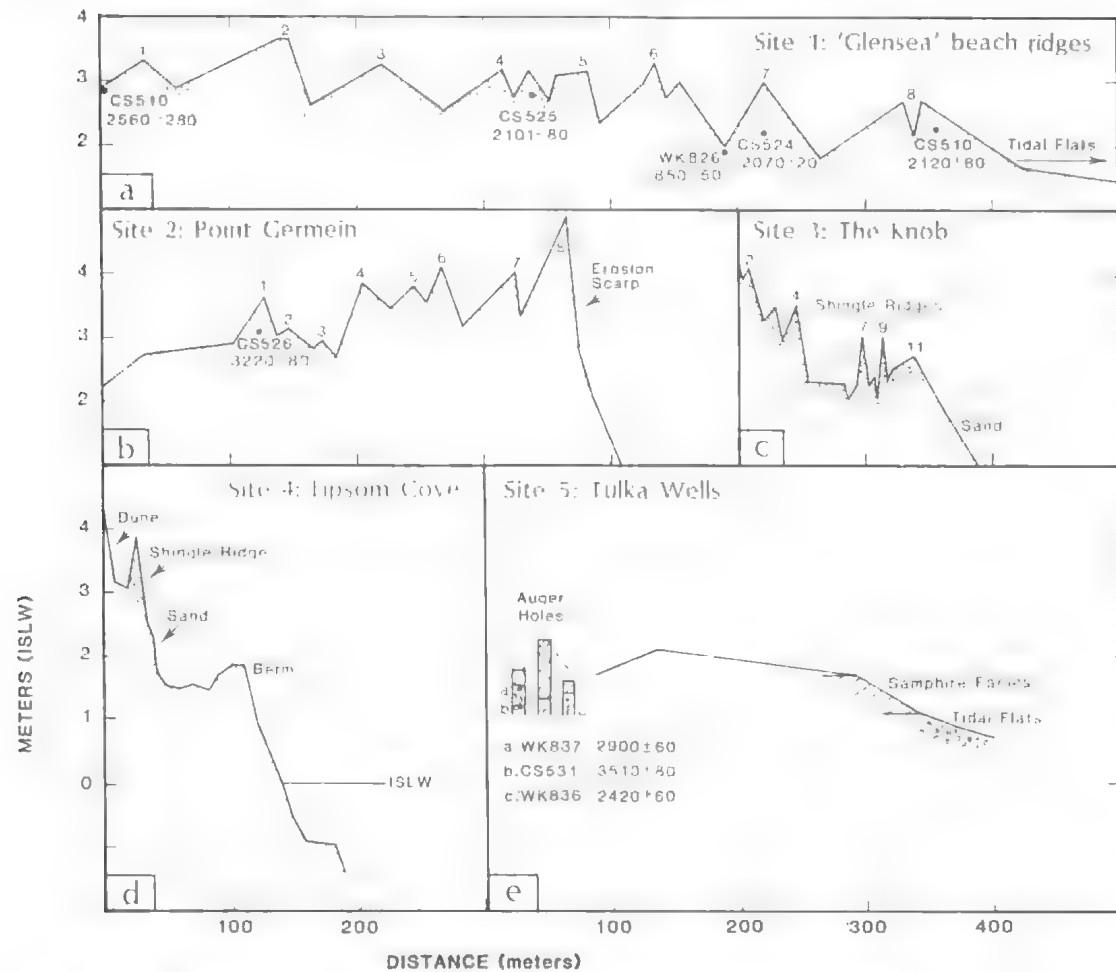


Fig. 3. Spencer Gulf field sites, Chronological ridge numbers indicated above some ridges.

Mount Dutton Bay.

On the north-western side of Mount Dutton Bay (site 9, Fig. 1) is a number of very low energy low beach ridge sites. One of these was surveyed and sectioned (Fig. 4e). The innermost sample (WK 833) dated at $>40,000$ yr BP indicating Pleistocene material. A sample obtained from tidal flat deposits below the base of the innermost ridge yielded a date of 6330 ± 90 yr BP (CS 530), the oldest Holocene date recorded in this study. This date confirms the arrival of the Holocene sea-level stillstand by at least 6.3 ka BP, in agreement with its arrival in Spencer Gulf (Belperio *et al.* 1984) and Australia in general (Hopley & Thom 1983). This date also is supported by the age of the first swale which dated at 4590 ± 80 yr BP, the third oldest date in this study. The elevation of the samphire — beach ridge, and tidal flat — samphire contact between ridge 1 and 2 (Fig. 4e) suggests a slight (~ 50 cm) fall in relative sea-level. The timing of this apparent fall however cannot be determined from the existing data.

Streaky Bay

Perlubie Beach (south)

Perlubie Beach (site 10, Fig. 1) is located in south-east Streaky Bay and consists of a 1 km wide plain of Holocene beach and foredune ridges (Fig. 5a). A single date was obtained from the shell-rich swash zone immediately behind the innermost Holocene ridge (CS 499). It dated at 3290 ± 90 yr BP, again suggesting a time gap between the stillstand and the onset of low energy beach ridge progradation.

Acraman Creek

The Acraman Creek (site 11, Fig. 1) region in northern Streaky Bay consists of a 10 km section of shoreline dominated by multiple episodes of recurved spit development and bayward beach ridge progradation (Fig. 5b). The shoreline at its maximum has prograded up to 3 km seaward. One date was obtained from the inner portion of the back barrier depression. Whole shell samples (CS

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TABLE 2. Radiocarbon Dates

Sample No.	Lab. No.	Location	CSIRO Environment km	Material	Elevation (in MSLW)	Age BP Yrs BP $\pm 1\sigma$	Corrected Age Yrs BP $\pm 1\sigma$
<i>a. Eyre Peninsula</i>							
Spencer Gulf							
4-2	CS 510	Glensea	1579	Back Swale	shell	3	2020 \pm 280
3-6	CS 511	Glensea	1579	Beach Ridge	shell	2.5	2580 \pm 80
4-1	CS 524	Glensea	1579	Beach Ridge	shell	3	2530 \pm 80
4-4	CS 525	Glensea	1579	Beach Ridge	shell	3	2470 \pm 80
4-5	WK 826	Glensea	1579	Swale	shell	2	1110 \pm 50
4-7	CS 526	Point Germein	1628	Beach Ridge	shell	3	3680 \pm 80
4-50	CS 531	Tulka Well	1856	Tidal Flats	shell	1	3970 \pm 80
4-49	WK 837	Tulka Well	1856	Tidal Flats	shell	1.6	3360 \pm 60
4-48	WK 836	Tulka Well	1856	Tidal Flats	shell	1.2	2880 \pm 60
<i>Coffin Bay</i>							
4-25	WK 828	Gate Waterhole	2089	Inter Barrier	shell	\sim 1	4150 \pm 190
4-24	WK 827	Morgans Landing	2089	Back Swamp	shell	\sim 1	3000 \pm 60
4-23	CS 527	Morgans Landing	2089	Beach Calcarenite	shell	Inter Tidal	3140 \pm 80
4-26	WK 829	Salt Waterhole-	2114	Back Swamp	shell	\sim 1	3900 \pm 60
4-27	WK 830	(Coffin Bay)	2114	Swash Deposit	shell	\sim 2	4390 \pm 60
4-28	CS 528	(Coffin Bay)	2114	Swash Deposit	shell	\sim 2	3650 \pm 80
4-37	CS 529	Yangie Island	2133	Inter Tidal	shell	0.7	3240 \pm 80
4-38	WK 832	Yangie Island	2133	Inter Tidal	shell	\sim 0.5	2540 \pm 60
4-39	WK 833	Mt Dutton Bay	2172	Inter Tidal	shell	1.7	$>40,000$
4-40	CS 530	Mt Dutton Bay	2172	Inter Tidal	shell	1.5	6790 \pm 90
4-41	WK 834	Mt Dutton Bay	2172	Inter Tidal	shell	1.3	5050 \pm 80
<i>Great Australian Bight</i>							
3-103	CS 499	Perlubie (south)	2544	Inner Beach Ridge	shell	?	3750 \pm 90
3-94	CS 503	Acarapman Creek	2583	Innermost Swale	shell	?	6110 \pm 90
3-88	CS 469	Point Collinson	2611	Shell Rock	shell	1-1.5	42,300 \pm 3000 42,300 \pm 2000
3-90	CS 469	Point Collinson	2611	Shell Rock	shell	1-1.5	37,900 \pm 1700 1400
3-70	CS 509	Eyre Island	2635	Inter Tidal	shell	\sim 1	1860 \pm 80
3-71	CS 508	Eyre Island	2635	Inter Tidal	shell	\sim 1	3300 \pm 90
3-72	CS 506	Eyre Island	2635	Inter Tidal	shell	\sim 1	3680 \pm 90
3-73	CS 505	Eyre Island	2635	Inter Tidal	shell	\sim 1	3770 \pm 160
3-26	WK 815	Laura Bay	2683	Beach Ridge	shell	2	6140 \pm 90
3-95	CS 504	Laura Bay	2683	Beach Ridge	shell	2	2740 \pm 90
3-96	WK 824	Laura Bay	2683	Beach Ridge	shell	2-3	2230 \pm 70
3-97	CS 502	Laura Bay	2683	Beach Ridge	shell	2	2520 \pm 90
3-98	CS 501	Laura Bay	2683	Beach Ridge	shell	2.5	2760 \pm 90
3-99	WK 825	Laura Bay	2683	Beach Ridge	shell	2.5	3480 \pm 60
3-100	CS 500	Laura Bay	2683	Swale	shell	2.5	4440 \pm 90
3-31	WK 816	Tourville Bay	2739	Beach Ridge	shell	2	2650 \pm 60
3-34	WK 817	Davenport Creek	2776	Chenier Ridge	shell	\sim 2	2470 \pm 90
3-35	WK 818	Davenport Creek	2776	Chenier Base	mangrove	\sim 1	2860 \pm 50
3-36	WK 819	Davenport Creek	2776	Chenier Base	mangrove	\sim 1	2570 \pm 50
3-37	WK 820	Davenport Creek	2776	Chenier Base	mud	\sim 1	2540 \pm 50
3-38	WK 821	Davenport Creek	2776	Intertidal	mangrove	\sim 0	2690 \pm 50
<i>b. Kangaroo Island</i>							
KI 13	WK 839	Mutripon Beach	42	Beach Ridge Swale	shell	1m	5040 \pm 70
KI 50	WK 842	Cygnal River	41	Shell Ridge	shell	2.5-3	3110 \pm 60
KI 51	WK 841	Cygnal River	41	Shell Ridge	shell	2.5-3	2750 \pm 50

1 = indicates uncorrected, estimate only

2 = Correction factor of 460 years used, see Howman & Harvey (1983).

503) gave a date of 5850 ± 90 yr BP the second oldest of the Holocene dates. This also supports the minimum age of the Holocene stillstand in this region at >6 ka BP.

Eyre Island

Eyre Island (site 12, Fig. 1), which partially blocks Smoky Bay is the only unconsolidated island in the Bight. It consists of a multiple series of onlapping recurved spits, beach ridges and low foredunes which surround a core of samphire — mangrove flats (Fig. 6). A transect was made across the westernmost and oldest of the existing ridges (Fig. 5c). The date obtained from the three swales and behind the present beach indicate that this section of the island began building around 3.8 ka BP and prograded to around 1.4 ka BP. This section is presently eroding as sediments are reworked eastward along both sides of the island to prograde the recurved spit complexes. As the island may have been reworked eastward prior to 4 ka BP the dates can only be used as a guide to the age of the oldest section of the existing island, and do not necessarily indicate the commencement of island formation.

Laura Bay

Laura Bay (site 13, Fig. 1) is a 2 km wide bay within Deeres Bay. It contains a 1.2 km wide beach ridge plain fronted by several hundred metre wide intertidal sand flats. The bay receives essentially no ocean wave energy as attested by the growth of mangroves on its northern sandflats. A series of seven dates obtained from two swales and the base of five ridges (Fig. 5d) suggests that progradation commenced after 4.0 ka BP (CS 500). A period of slow progradation (100 m between 4-3 ka BP, ridges 1 and 2), was followed by rapid progradation (500 m) between 3-2 ka BP (Fig. 5d). All ridges are within the reach of present storm swash elevations and do not suggest any apparent change in sea-level. Like the Glensea ridges, the 2.3 ka age for the outer active ridge (6) may indicate age contamination by older shells, and hence a younger age may be appropriate.

Tourville Bay

Tourville Bay (Site 14, Fig. 1) is the westernmost enclosed bay in S. Aust. and contains the westernmost mangrove woodland in South and southern Australia. A total of five dates were obtained in the bay, four from Davenport Creek and one from the northern side of the bay (Fig. 5e). Davenport Creek consists of a 10 km² mangrove woodland described by Butler *et al.* (1977), within which lie three discontinuous cheniers (Fig. 7). The

second of the three cheniers was sectioned and provided a sequence of three dates (WK 820, 818, 819, Fig. 5f). These dates confirm the emplacement of this second chenier at between 2.5 and 2.0 ka BP, and the development of the underlying tidal flats by 2.5 ka BP. Mangrove stumps on the south side of Davenport Creek, presently being buried by dune transgression dated at 2690 ± 50 (WK 821), contemporaneous with the chenier base mangroves. The date on the northeast shore of Tourville Bay was obtained from the intertidal base of the innermost beach ridge (WK 816). Its date of 2190 ± 60 yr BP coincides with the development of the second chenier. These dates are confirmed by the results of Belperio *et al.* (1988) who present the results of 13 vibrocores across Tourville Bay. They found the basal *Posidonia* seagrass facies began accumulating about 6800 yr BP, with the embayment largely infilled by 5000 yr BP. Beach ridge formation followed the mantling of the seagrass banks by intertidal and mangrove facies. Their innermost and single beach ridge date of 1840 yr BP is in agreement with our findings.

Kangaroo Island

Most of the Kangaroo Island coast is typified by high bedrock and calcarenous cliffs exposed to high wave and wind conditions. However the north east leeward part of the island contains three embayments — the Bay of Shoals, Western and Eastern Coves which offer varying degrees of low energy Holocene shoreline progradation. Western Cove has experienced the most substantial progradation with sediment being delivered alongshore from its eastern and western arm, as well as from the Cygnet River and *in situ* deposits. Four sites were examined around the shoreline (Figs 1, 8).

Brownlow

A series of five, low, shelly, swash-deposited bench ridges was surveyed at Brownlow (site 15, Fig. 1; Fig. 8a). Their uniform elevation suggests no apparent change in sea-level. No dates have been obtained.

Brownlow golf course

Seven low shelly ridges were surveyed immediately south of the Brownlow golf course (site 16, Fig. 1) and again their relatively uniform elevation gives no indication of sea-level change (Fig. 8b).

Cygnet River

A series of low, discontinuous beach ridge and possibly cheniers were surveyed 1 km south of the Cygnet River mouth (site 17, Fig. 1). The two ridges

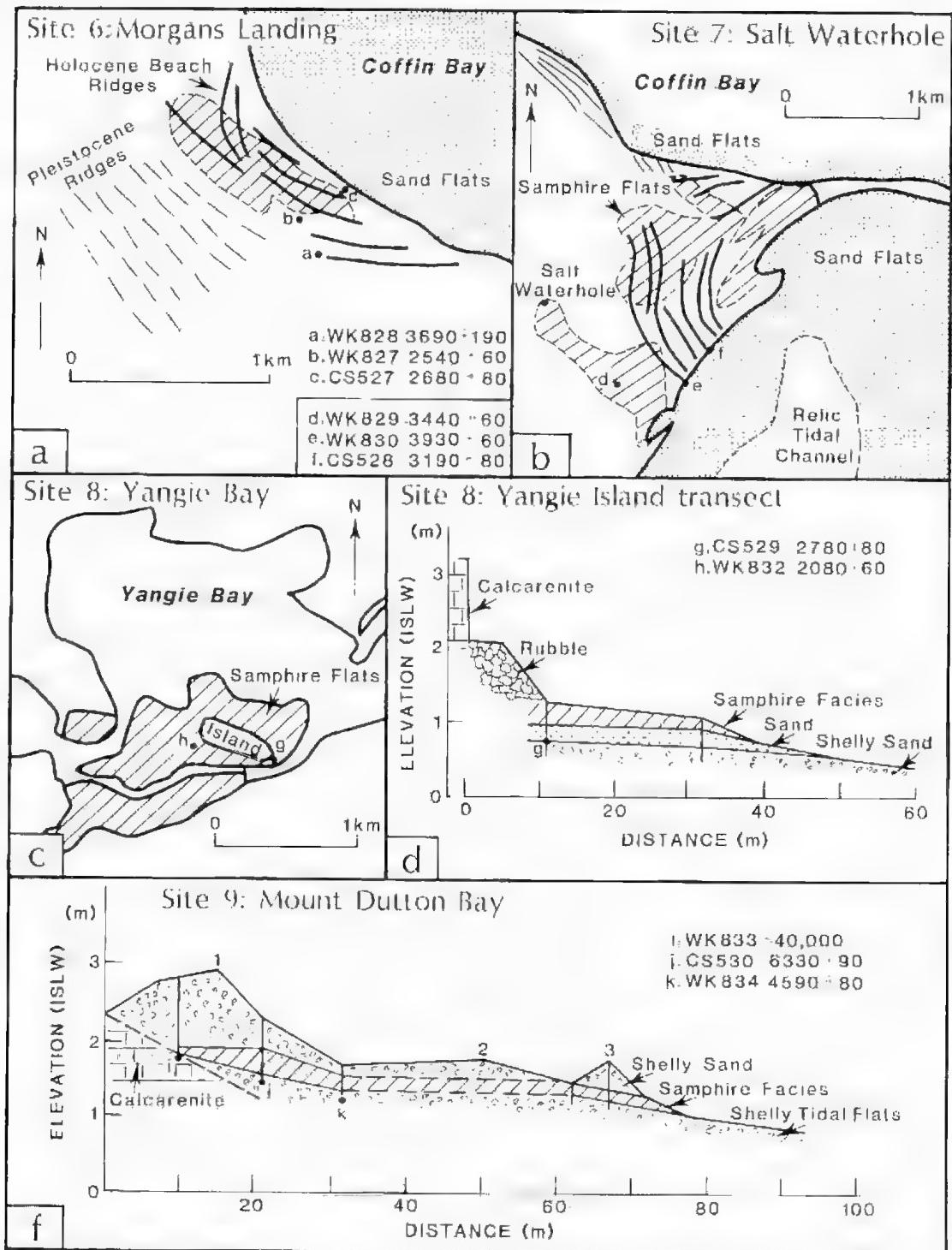


Fig. 4. Coffin Bay field sites. Sites 6, 7 and 8 were not surveyed. Sketches based on 1:10,000 aerial photographs.

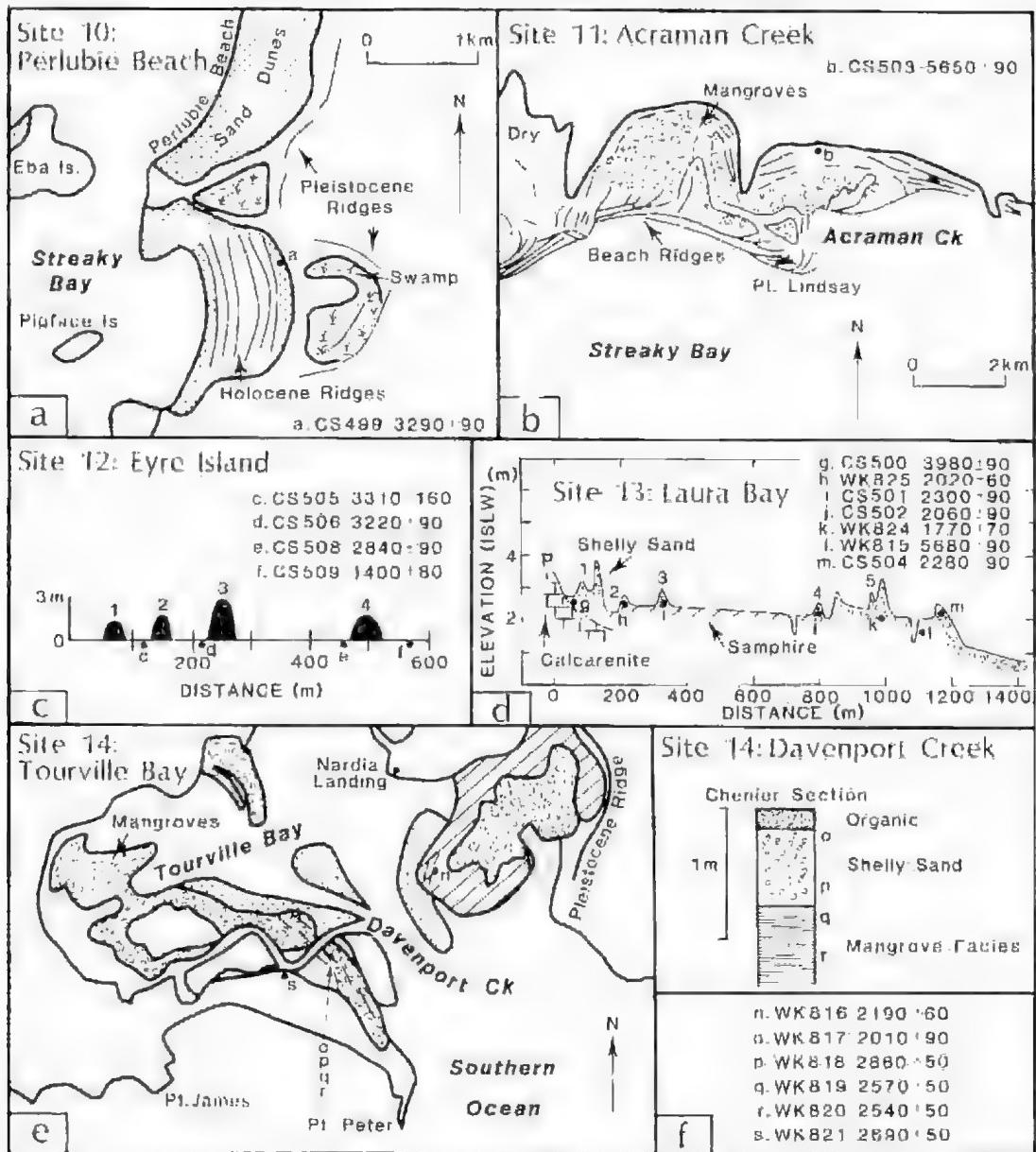


Fig. 5. Western Eyre Peninsula field sites. Sites 10, 11 and 14 not surveyed. Sketches based on 1:10,000 aerial photographs. Site 12 survey elevations suspect, distances correct. Chronological beach ridge numbers given for sites 12 and 13.

yielded dates of 2650 + 60 and 2290 + 50 yr BP (WK 840, WK 841). The ridges are now fronted by 300 m of densely vegetated samphire flats (Fig. 8c). Their distance from the present shoreline and the elevation of the samphire flats could have resulted from a slight fall in sea-level subsequent to their formation. However this cannot be confirmed from the present data.

Morrison Beach

Two sites were examined at Morrison Beach (sites 18 and 19, Fig. 1). In a waterhole at the eastern end

of the beach (Site 18) the elevation of intertidal shingle exposed in the waterhole is ~0.5 m higher than the present beach shingle (Fig. 8d), and could be attributed to a slight fall in sea-level. However the elevation of the inner shingle lies within the reach of storm swash activity.

The beach-foredune ridge plain at Morrison beach consists of a 2–3 km wide plain that has prograded northward and westward into the bay (Fig. 1; Morris 1976). Shells obtained from a swale behind one of the innermost ridges (site 19) (WK 839) dated at 4580 + 70 yr BP, indicating that



Fig. 6. A view looking eastward along the Smoky Bay side of Eyre Island. The subtidal sand-flats are backed by a low energy reflective beach, and multiple recurved spits/beach ridges with samphire flats and mangroves composing the core of the island.



Fig. 7. A view southeast across Tourville Bay shows the Davenport Creek tidal channel and sandflats backed by mangrove woodlands and the discontinuous chenier ridges (C). Active dune transgression (D) in the south is burying the mangroves.

TABLE 3. Beach ridge molluscs in approximate order of abundance

a, Intertidal mollusc species commonly found in Eyre Peninsula Holocene beach ridge and swale deposits. All these species are associated with low energy mud/sand flat situations, generally with associated *Zostera* beds or silted rocks etc . . . *Coxiella* sp. is usually associated with salt pans or salty lakes. *Bembicium melanostoma* and *Salinator fragilis* are found on mud flats at the upper intertidal zone in sheltered estuarine areas. *Anadara trapezia* is usually associated with *Zostera* beds; it is extinct in S. Aust.

b, Rocky shoreline species (also found in Eyre Peninsula beach ridges).

c, Kangaroo Island beach ridge molluscs, primarily in Western Cove region.

a	b	c
<i>Katelysia peroni</i> (Lamarck)	<i>Tellina (Macomona) deltoidalis</i> (Lamarck)	<i>Katelysia scalarina</i> (Lamarck)
<i>Katelysia scalarina</i> (Lamarck)	<i>Trichomya hirsuta</i> (Lamarck)	<i>Katelysia peroni</i> (Lamarck)
<i>Amesodesma erycinaea</i> (Lamarck)	<i>Cominella eburnea</i> (Reeve)	<i>Katelysia rhytophora</i> (Lamarck)
<i>Amesodema cuneata</i> (Lamarck)	<i>Austrocochlea constricta</i> (Lamarck)	<i>Zeacumanties diemenensis</i> (Q & G)
<i>Spisula trigonella</i> (Lamarck)	<i>Phasianotrochus rutilus</i> (A. Adams)	<i>Mesodesma cuneata</i> (Lamarck)
<i>Anadara trapezia</i> (Deshayes)	<i>Sanguinolaria biradiata</i> (Wood)	<i>Fulvia tenuicostata</i> (Lamarck)
<i>Brachidontes erosus</i> (Lamarck)	<i>Mactra Pura</i> (Deshayes)	<i>Austrocochlea concamerata</i> (Wood)
<i>Batillariella estuarina</i> (Tate)	<i>Fulvia tenuicostata</i> (Lamarck)	<i>Nassarius pauperata</i> (Lamarck)
<i>Zeacumanties diemenensis</i> (Quoy Gaimard)	<i>Ostrea angasi</i> (Sowerby)	<i>Pisulatrigonella</i> (Lamarck)
<i>Salinator fragilis</i> (Lamarck)	<i>Bembicium cf. auratum</i> (Quoy & Gaimard)	<i>Batillaria estuarina</i> (Tate)
<i>Thalotia conica</i> (Gray)		<i>Nerita atramentosa</i> (Reeve)
<i>Prothalotia</i> sp.		<i>Brachydontes erosus</i> (Lamarck)
<i>Bembicium meeanostoma</i> (Gmelin)		<i>Tellina (Macomona) deltoidalis</i> (Lamarck)
<i>Coxiella</i> sp.		<i>Cominella lineolata</i> (Lamarck)
<i>Phasianella australis</i> (Gmelin)		<i>Cominella eburnea</i> (Reeve)
"Bulla botanica" Hedley		<i>Austrocochlea concamerata</i> (Wood)
<i>Diala</i> sp.		<i>Salinator</i> sp.
		<i>Diala</i> sp.
		<i>Bittium</i> sp.

initiation of this substantial and continuing shoreline progradation commenced by 4.5 ka BP.

Shore Platform Evidence

Shore platforms cut into Pleistocene beach and dune calcarenite are widely distributed around the western Eyre Peninsula and Kangaroo Island open coast. Whilst shore platforms are highly questionable indicators of sea-level (Twidale *et al.* 1977; Hopley & Thom 1983) they do warrant brief attention in regard to possible changes in Holocene sea-level in the Bight and Kangaroo Island.

Three platforms in the Bight were examined for evidence of Pleistocene sea-level (Buckley *et al.* 1987). Two of these platforms contained a well defined upper, inactive Pleistocene platform, fronted by a wide active intertidal Holocene platform (Merdayrah and Clare Bay; Fig. 1). Subsequent low altitude aerial reconnaissance of the entire Eyre Peninsula and Bight by ADS and DGF revealed the existence of relict elevated platforms, presumably of Pleistocene age along much of the calcarenite coast. Active horizontal shore platforms occupy 440 km of the Eyre Peninsula coast (Short *et al.* 1986) and are usually located intertidally close to mean sea-level. All western Eyre Peninsula platforms examined possessed a single active

platform surface. On Kangaroo Island, however, Short & Fotheringham (1986) describe a Pleistocene platform at Pennington Bay (site 20, Fig. 1) fronted by two Holocene platforms at different elevations (Fig. 8e). The upper platform (No. 1, Fig. 8e) lies 50 cm above the lower platform (No. 2). The difference in elevation and abrupt drop from platform 1 to 2 may be a result of a slight fall in sea-level (~50 cm) producing a lowering of the level of saturation and hence platform erosion surface.

Discussion

These data have implications both for the evolutionary history of the low energy beach ridge sequences and for mid-late Holocene sea-level history in the Bight and on Kangaroo Island.

Beach Ridge Progradation

The initiation of beach ridge progradation at nine of the 12 sites dated did not commence until 4 ka BP and in some areas as late as 2 ka BP (Fig. 9). Most sites indicate an hiatus between the Holocene sea-level stillstand and inner ridge building of up to 4 ka. This is in general agreement with Burne (1982) who found that in northern Spencer Gulf the

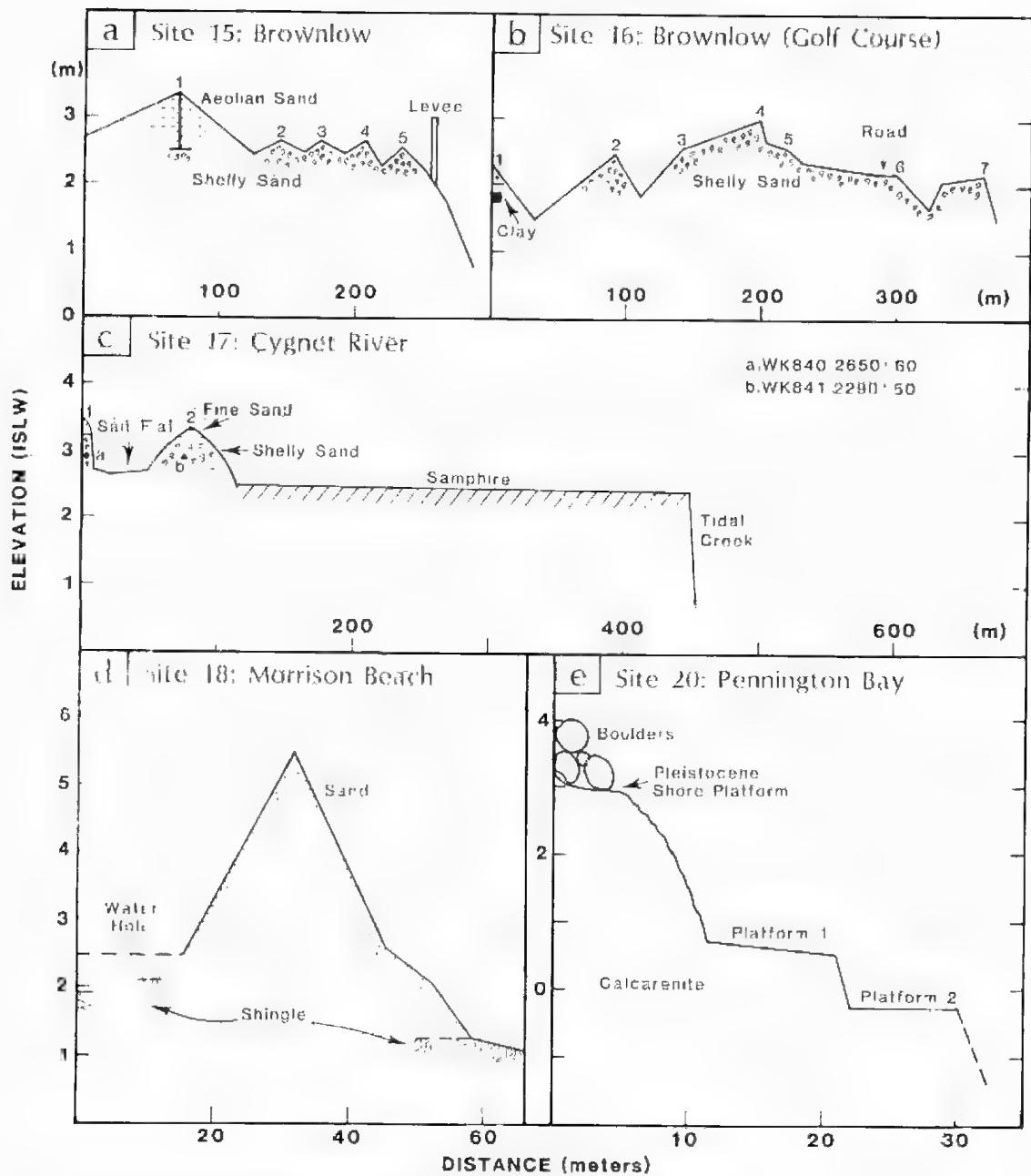


Fig. 8. Kangaroo Island field sites: Beach ridges are numbered chronologically.

development of low energy beach ridge plains awaited sufficient subtidal carbonate production and as a result progradation did not commence until 4–3 ka BP. Belperio *et al.* (1988) also concluded that carbonate secreting organisms aggrade and prograde the subtidal sand banks in association with the subtidal seagrass facies. Once the banks accumulate to low water level, subsequent intertidal and beach ridge progradation can occur. They

found this sequence at Tourville Bay on Eyre Peninsula as well as several sites in Spencer and St Vincent Gulfs.

In Gulf St Vincent, Bowman & Harvey (1986) found that the extensive Le Fevre Peninsula beach ridges have been prograding continuously over the past 7000 years with pulses in ridge formation apparently linked to longshore (northward) sediment supply. This higher energy west facing

system (modal H_b = 0.5 m) represents a transition between the low energy beach ridges discussed in this paper and the high energy open coast regressive deposits which experienced rapid progradation following the stillstand. Their mode and sequence of evolution of the Peninsula is therefore not directly applicable to the lower energy systems of all which experienced a substantial lag in ridge development.

On the two sites where a sequence of beach ridges was dated (excluding Eyre Island) the youngest ridges dated 2010 yr BP (Glensea) and 1770 yr BP (Laura Bay), suggesting that ridges are either not currently prograding or older material is being deposited during ridge building. Whilst ridge cessation is in agreement with sedimentation models in higher energy sites in south-east Australia (Thom *et al.* 1981), it is surprising in an environment where most sediments are derived from *in situ* carbonate production from fronting intertidal and subtidal sand flats, the so called 'carbonate factory' (Burne 1982). In northern Spencer Gulf, Burne found periods of shoreline (i.e. sandflat) progradation, alternating with beach-ridge progradation. The most notable shoreline progradation was between 3 and 2 ka BP. On the Eyre Peninsula, however, that was the period of maximum beach ridge construction. A similar contrast applied to the period from 2 ka BP to present; beach ridges in the north-east Spencer Gulf prograded, while those in the Eyre appear to have remained static. Evidently more information is required before general models of S. Aust. beach ridge-sandflat progradation can be clarified.

Eyre Island has a slightly younger outer ridge (1400 yr BP) and the island is continuing to develop new recurved spits. However this may be accounted for by erosion and downdrift reworking of island sediments rather than external sand supply.

Holocene Sea-Level

The exact timing of the Holocene sea-level maximum cannot be resolved from these dates. However the date of 6330 ± 90 yr BP from Little Douglas as well as the 5650 ± 90 yr date from Aceman Creek lend support to the general curve adopted by Belperio *et al.* (1984) for Spencer Gulf and Hopley & Thom (1983) for Australia as a whole. That is, it appears that the sea-level reached its present position by 6.3 ka BP in the Great Australian Bight.

In evaluating evidence for relative sea-level history during the mid to late Holocene, tectonic differences between the three main regions, the Bight, Spencer Gulf and Kangaroo Island must be taken into account. The most stable region appears to be western Eyre Peninsula (the Bight). Tectonic stability is suggested by the widespread occurrence of the c. 2–3 Pleistocene shore platforms (Buckley *et al.* 1986), the continuity of the presently active shore platforms, the single intertidal solution notches in limestone cliffs in Coffin Bay and the evidence from dated beach ridge and tidal sites (Figs 4, 5). In the Bight the sea-level maximum was reached at least by 5650 yrs BP (Fig. 5b) and has been stable since. In northern Spencer Gulf there is, however, evidence for Holocene tectonism. Belperio *et al.* (1984) proposed a sea-level curve for northern Spencer Gulf which has a stillstand being reached at c. 6.5 ka followed by an abrupt fall to present sea-level at 1.7–1.6 ka BP. They attribute this relative fall to local tectonism. The present Spencer Gulf data are not sufficient to add to the Belperio *et al.* curve and may well be tectonically or isostatically distinct. The Glensea beach ridges and swales slope seaward (Fig. 3a); however this is not conclusive evidence for a slight fall in sea-level without subsurface morphostratigraphy. It could also represent a decrease in wave-energy as the 1 km wide intertidal and subtidal sand flats accumulated. Likewise, while other Spencer Gulf sites together with Yangie Island and Mount Dutton Bay sites may suggest a modest fall in sea-level (<1 m), errors inherent in surveying, facies identification and elevation, dating and establishing reliable datums, place all of the possible changes within the sampling error bands. Consequently there is no conclusive evidence for a small relative fall in sea-level. If any has occurred it would be only on the order of a few decimetres. Together with the Bight data this suggests a relatively stable sea-level since the sea-level maxima at or prior to 6300 yr BP.

Summary and Conclusions

The following sequence of events appears to have occurred along the low energy Bight, Eyre Peninsula and Kangaroo Island coasts since the Holocene sea-level stillstand.

7–6 ka BP. The stillstand was achieved by at least 6330 ± 90 yrs. BP and most likely by 6.6–6.4 ka BP based on evidence from northern Spencer Gulf (Belperio *et al.* 1984).

6–4 ka BP. Following the stillstand most low energy sections of coast experienced minimal shoreline progradation. Exceptions were areas where shingle was immediately available, particularly in Spencer

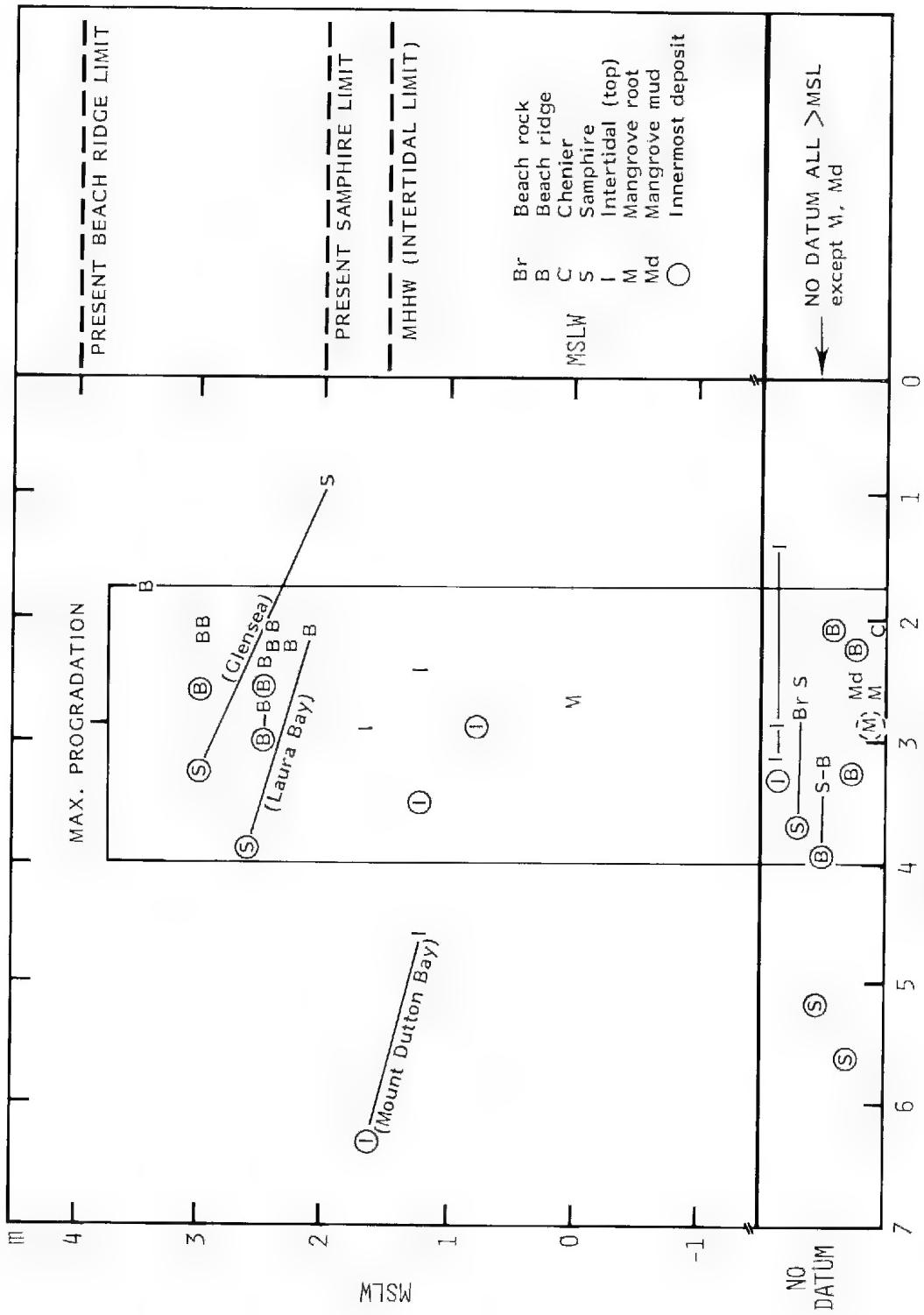


Fig. 9. Plot of Holocene dates versus elevation for low energy beach ridge sites on Eye Peninsula and Kangaroo Island.

Gulf. In these areas storm shingle ridges were developed following the stillstand. Whilst no dates are available from the present data, dating of similar ridges in northern Spencer Gulf by Burne (1982) found progradation commenced around 6 ka BP. Only three beach ridge sites (Mount Dutton Bay, Aeraman Creek and Morrison Beach) have back barrier deposits older than 4 ka BP. No beach ridges were dated prior to 4 ka BP. However prior to beach ridge formation the substantial inter- to sub-tidal sand flats would have to be building during this period.

4–2 ka BP. This was apparently a period of major beach ridge and limited crenier development in Spencer Gulf, the Bight and on Kangaroo Island. The commencement of ridge construction has been dated as early as 3930 ± 60 yr (WK 830) in Collin Bay (Fig. 4b) and as late as 2190 ± 60 (WK 816) in Tourville Bay (Fig. 5c). The most logical explanation of this surge in ridge formation is the development of the inter- to sub-tidal carbonate platforms and sediments required to both support and supply sediment for ridge development possibly coupled with a slight fall in sea-level.

2–0 ka BP. Fig. 9 is not representative of low energy deposits as many of the samples were selected to date the oldest ridge/swale. All that can be said is that on the two sequences dated, the youngest ridge dated at 2010 and 1770 yr BP (Figs 3a, 5d). However there is abundant evidence of contemporary ridge formation, particularly in areas of recurved spits (eg. Eyre Island, Aeraman Creek, St Peter Island). Possible explanations for the outer ridge is that in areas of shore normal sediment supply there is a precept hiatus in ridge formation, or possibly older shells are being incorporated in outer ridge deposits to give an anomalous age. Whatever the cause these systems require further investigation. In conclusion:

1. Low energy beach ridges and some creniers occupy 65 km (4%) of the western Spencer Gulf and Bight coast, particularly in the larger more sheltered bays. They also occupy 14 km of coast in the north-east of Kangaroo Island. Most sequences consist of 2–10 ridges (mean 4.5 in Spencer Gulf).
2. The ridges are composed of predominantly carbonate shell detritus (Table 3) apparently

sourced and reworked from the adjacent inter- and sub-tidal sandflats and adjacent rocky shores.

3. Ridge formation awaited the construction of the underlying inter- and sub-tidal sandflats. The sandflats were required both to provide a platform for ridge building, as well as a ready supply of material. The increasing prominence of carbonate sediments is reflected in the gulfward increase in carbonate content of the Glensea ridges (Fig. 3a).
4. Once the intertidal sandflat platforms were constructed, ridge formation often was rapid. In places several ridges separated by wider swales were deposited in several hundred years, usually between 4–2 ka BP. However age contamination of outer ridges by older shells may mask a younger age and hence longer period of ridge building.
5. At present most active ridge formation is occurring in areas of longshore supply, resulting in the construction of multiple recurved spits. Shore normal supply may be negligible resulting in an apparent hiatus in ridge construction or conversely older material is being incorporated to provide anomalous ages.
6. The sea-level stillstand occurred prior to 0.2 ka BP and has been relatively stable since; particularly in the Bight. There is inconclusive evidence of a slight (<1 m) fall in sea-level in Spencer Gulf and a (0.5 m) fall on Kangaroo Island in the late Holocene.

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THE OCCURRENCE OF A DIPROTODONTID MARSUPIAL REFERABLE TO *EUOWENIA GRATA* DE VIS IN WESTERN NEW SOUTH WALES

BY N. S. PLEDGE*

Summary

A complete last upper molar (M^5) and fragments of several other teeth found in a bore on the Talyawalka Anabranch, east of Menindee, N.S.W., are identified as the Pliocene species *Euowenia grata* De Vis. *Euowenia grata* is redescribed and refigured, and the new M^5 is compared with the equivalent teeth of *Diprotodon optatum*, *Zygomaturus trilobus*, *Meniscocephalus mawsoni*, *Nototherium mitchelli* and *Palorchestes azael*. The Talyawalka specimen extends the range of *Euowenia grata* by almost 1000 km and suggests a Pliocene age for the deposit.

KEY WORDS: diprotodontid marsupial, *Euowenia*, *Diprotodon*, *Zygomaturus*, *Meniscocephalus*, *Nototherium*, *Palorchestes*, Talyawalka, Menindee, New South Wales, Pliocene.

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Summary

PLEDGE, N. S. (1989) The occurrence of a diprotodontid marsupial referable to *Euowenia grata* De Vis in western New South Wales. *Trans. R. Soc. S.Aust.* 113(3), 163–168, 30 November, 1989.

A complete last upper molar (M^3) and fragments of several other teeth found in a bore on the Talyawalka Anabranch, east of Menindee, N.S.W., are identified as the Pliocene species *Euowenia grata* De Vis. *Euowenia grata* is redescribed and refigured, and the new M^3 is compared with the equivalent teeth of *Diprotodon optatum*, *Zygomaturus trilobus*, *Meniscocephalus mawsoni*, *Nototherium mitchelli* and *Palorchestes azael*. The Talyawalka specimen extends the range of *Euowenia grata* by almost 1000 km and suggests a Pliocene age for the deposit.

KEY WORDS: diprotodontid marsupial, *Euowenia*, *Diprotodon*, *Zygomaturus*, *Meniscocephalus*, *Nototherium*, *Palorchestes*, Talyawalka, Menindee, New South Wales, Pliocene.

Introduction

De Vis established the species *Owenia grata* (De Vis 1887), for a skull and jaws (Fig. 3, QM F519) found at Chinchilla, Queensland. Later he renamed it *Euowenia* (De Vis 1891) after finding the earlier name to be preoccupied by an annelid worm. At the same time, he named a second species, *Euowenia robusta*, for a set of dentaries found at Freestone Creek, near Warwick, Qld, in Pleistocene alluvium. Woods (1968) suggested that *Euowenia robusta* is a junior synonym of *Nototherium inerne* which could effectively restrict *Euowenia* to specimens from the Chinchilla Sand, and to a Pliocene age (Woods 1960; Bartholomai & Woods 1976).

Euowenia grata occurs with certainty only at Chinchilla (Stirton *et al.* 1968). M. Archer has informed me (pers. comm. 3.xi.1975): "In many cases, specimens should more honestly be referred to merely as undetermined small nototherines", and there is no evidence at present for any Pleistocene occurrence. Recently, *Euowenia* has been listed (Telford, Williams & Wells 1986) in the Plio-Pleistocene Kanunka local fauna at Lake Kanunka, South Australia, but this record needs confirmation.

The purpose of this note is to record a new occurrence of the species well beyond its previously known locality.

Material and Methods

In 1969, Mr D. Walker of Talyawalka Station east of Menindee, New South Wales, presented to the South Australian Museum some unusual tooth fragments found in the sludge from a newly-drilled water bore in "White Water Lake" (32°25'S,

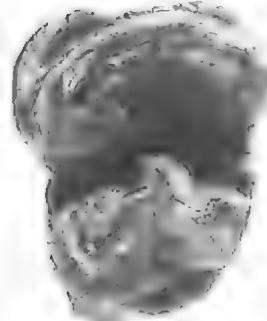


Fig. 1. Locality map. White Water Lake, Talyawalka Anabranch, New South Wales.

143°18'E) on the Talyawalka Anabranch of the Darling River (Fig. 1).

The new specimen is very fragmentary, comprising the complete left M^3 , two enamel fragments with differing degrees of wear, believed to be anterobuccal corners of the protolophs of M^1 and M^2 of the same tooth row, the anterobuccal corner of the metaloph of M^1 , the anterior half of M_2 , an unidentifiable molar fragment and a fragment of incisor. Because of the poor quality of De Vis' figure (De Vis 1887), the new specimen was for several years considered by the author to be a possible very large new species of *Palorchestes*, because it had a fairly distinct midlink between the lophs. However, direct comparison with a cast of the upper dentition of *Euowenia grata* (holotype QM F519) by courtesy of Dr M. Archer, has now proven its identity. The specimen also has been

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**A****B****C**

compared with teeth or casts of *Diprotodon optatum*, *Zygomaturus trilobus*, *Meniscocephalus mawsoni*, *Notatherium mitchelli* and *Palorchestes australis*.

Material is from the South Australian Museum, Adelaide (SAM), Queensland Museum, Brisbane (QM) and British Museum (Natural History), London (BMNH).

The status of the genus *Euowenia* is thought to be in doubt and in need of major revision (Archer & Wade 1976), but until this is done it is felt that a redescription of the species is desirable, based partly on this new material. Tooth notation follows Archer (1978).

SYSTEMATICS

Euowenia grata De Vis
FIGS 2-4.

Owenia grata De Vis, 1887, p. 100, pl. I-IV

Upper premolar two-rooted, about half the length of M^2 and triangular (De Vis 1887, 1888). Protocone slightly smaller than parametacone. Protocone and anterior part of parametacone joined by narrow transverse loph to form short side of a right triangle. Buccal side formed by buccal crest from parametacone to anterior end of the

tooth. Third side formed by anterolingual cingulum. Small deep central basin with rugose enamel.

Upper molars large (Tables 1, 2) and bilophodont, with lophs convex forwards and somewhat tumid with incipient midlink development — postproto-crista posteromedially from protocone and pre-metacrista(?) extending anteromedially from metacone. Midlink development virtually absent in M^2 but increases slowly to its greatest extent in M^3 where pre- and post-cristae are confluent for a few millimetres vertically. M^{2+3} subrectangular; M^3 trapezoidal, with metaloph about three-quarters width of protoloph. In M^1 and M^3 , metaloph forms distinct dog-leg bend where midlink joins it. Anterior cingulum extends full width of tooth, but is longer at its lingual end. Posterior cingulum narrow, particularly on M^3 where small pocket may be formed by weak postmetacrista. Only trace of a lingual cingulum may be seen, at bottom of transverse valley. Buccal cingulum better developed, across mouth of transverse valley.

Lower molars more rectangularly elongate than uppers. Both protolophid and hypolophid are oblique and concave anteriorly. Protoconid end of protolophid enlarged by development of preproto-cristid extending anteromedially. Similarly, hypoconid end of hypolophid is enlarged by cristid obliqua which forms posterior half of weak mid-

TABLE 1. Cheek Teeth Dimensions, *Euowenia grata*

Except for the premolar, measurements are made in planes parallel to and normal to the lingual edge of the tooth.

	SAM P14506		QM F519 (epoxy cast)			SAM P14506	
	LM ₁	LP ²	LM ²	LM ³	LM ³	LM ⁵	LM ⁵
A-p Length	—	15.0	26.5	32.6	36.2	35.7	34.8
Ant. Diam.	19.3	—	20.1	26.2	30.3	28.7	27.7
Post. Diam.	—	15.7	21.2	25.9	28.4	23.2	23.1

TABLE 2. *Euowenia grata* Dimensions as given by De Vis (1887)

These are not directly comparable with those in Table 1, as M^3 for example is apparently measured along the outer edge.

	P ₂	M ₁	P ³	M ³
Length	14.5	34.5	15.0	38.0
Max. Breadth	8.5	22.0	14.5	29.5

Fig. 2. *Euowenia grata* De Vis. Left upper molar M_1 of SAM P14506. Stereopair photographs: a) Occlusal; b) buccal; c) lingual view. Scale = 1 cm.



FIG. 3. *Euowenia grata* De Vis. Holotype palate and dentaries, QM F519. Scale bar = 10 cm.

link. In the holotype, lowest part of midlink is intact in last molar (De Vis 1887). Anterior cingulum almost full width of tooth. Postcingulum divided unequally into two parts at its highest point by fine submedian posthypocristid.

Comparison with other species

The Talyawalka specimen may be compared with this (Table 1) and other diprotodontoids.

The upper molar M^5 is the same size as that of the holotype of *Euowenia grata*, and same order of size as *Meniscocephalus mawsoni*. It is smaller than *Zygomaturus trilobus* and slightly more than half the length of *Diprotodon optatum*.

The Talyawalka tooth differs from *Diprotodon* (SAM P23406, Lake Callabonna) in: its much smaller size, relatively higher crown, more convex protoloph, slightly narrower precingulum with greater development at the lingual end, a buccal cingulum across the end of the transverse valley, a narrow but strongly developed postcingulum, the

absence of cementum, and particularly the presence of a Y-shaped hypoloph formed by a distinct premetacrista.

It differs from *Zygomaturus* (SAM P29889, Naracoorte) in: its smaller size (about three-quarters the length), shorter precingulum, absolutely higher lophs, thicker lophs, presence of a distinct buccal cingulum across the transverse valley, deeper and more acute transverse valley, distinct premetacrista, more distinct postmetaloph-pocket, and presence of rugose/punctate enamel.

It differs from *Nototherium mitchelli* (cast of BMNH M5002) in: its smaller size, its longer and better developed precingulum, presence of a buccal cingulum across the transverse valley, relatively higher lophs, presence of a premetacrista, and better developed postcingulum.

It differs from *Meniscocephalus* (SAM P13647, of which M^3 is unknown) in slightly smaller size, higher lophs, presence of distinct premetacrista, and narrow postcingulum.



Fig. 4. *Euowenia grata* De Vis. Cast of left upper maxillary tooth row of holotype, QM F519.

It differs from the holotype of *Euowenia grata* (cast of QM F519) in: having a distinct buccal cingulum with two small (one twice as big as the other) cusps across the transverse valley, and a more distinct postmetaphyseal-pocket.

It differs from *Potorous uzael* (QM F773, *sic!* De Vis 1895) in: its larger size, relatively greater length, lack of a forelink, presence of a strong buccal cingulum across the transverse valley, strong postcingulum, and absence of a complete midlink.

The new specimens (SAM PI4506) agree closely with the holotype, considering the difference in degree of wear and preservation. In M^3 , the enamel is just breached so that a good indication of the height and form of the teeth can be gained. The lophs are high (equal to the width of the tooth) and stout so that the transverse valley is particularly deep and narrow, a narrowness accentuated by the bend caused by the premetacrista. Together, the metaloph and premetacrista have a distinct Y-form. *Contra* De Vis (1887), I found no indication of a forelink on the upper molars of the holotype cast, but there is a slight protuberance in this position on the new specimen of M^3 .

The molar enamel is notably rugose and punctate, similar to that of *Diprotodon* and *Euryzygoma* (Archer 1977). In the worn M_2 fragment, the anterior cingulum is heavily abraded by interdental apposition and has a small cusp developed at the anterolingual corner. The "midlink" is discontinuous and does not cross the transverse valley as an integral structure.

The incisor is too fragmentary to describe, save that it would be roughly circular in section with a diameter of at least 22 mm. Only a portion of the root is preserved and, from De Vis' description (1887), it could be either upper or lower I_1 .

Discussion

The teeth came from a depth of about 28 m, in a 1.5 m thick bed of coarse, yellow-brown dirty quartz sand, below sandy clay. The age is uncertain, but an early Pleistocene, or even Pliocene, age is possible, based on the absence of the species from late Pleistocene surficial deposits nearby — lunette sands dated at 25,300 years BP at Lake Menindee (Telford 1967) and 32,000 years old at Lake Mungo (Barbetti & Allen 1972). Although speculative, this determination is supported by the Pliocene age of the holotype (Woods 1960). The specimen extends the known range of the taxon by almost 1000 km.

It seems that the bore drill struck a more-or-less complete skull and jaws of *Euowenia* because all fragments appear to relate to a single individual, there being no duplication of elements.

Conclusions

These fossil teeth, recovered from a water bore on the Talyawalka Anabranch, east of Menindee, N.S.W., match those of *Euowenia grata* (De Vis) and, because they are less worn than the holotype, add to the knowledge of the species. The occurrence extends the known range of the species.

Acknowledgments

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TRANSACTIONS OF THE
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**PARASITOIDS OF *URABA LUGENS* WALKER (LEPIDOPTERA:
NOCTUIDAE) IN SOUTH AUSTRALIA, WITH DESCRIPTION OF TWO
NEW SPECIES OF BRACONIDAE**

*BY A. D. AUSTIN & G. R. ALLEN**

Summary

Information is presented on the large complex of hymenopteran and dipteran parasitoids associated with *Uraba lugens* Walker (the gumleaf skeletonizer) in South Australia. A key to the 22 species involved is presented, along with notes on identification and relationships with their host. Two species of microgastrine braconids are described, *Cotesia urabae* sp. nov. and *Dolichogenidea eucalypti* sp. nov.; both are parasitoids of the larval stages of *U. lugens*.

KEY WORDS: *Uraba lugens*, Noctuidae, parasitoids, hyperparasitoids, Braconidae, Ichneumonidae, Aphelinidae, Chalcididae, Elasmidae, Eulophidae, Eurytomidae, Eupelmidae, Trichogrammatidae, Tachinidae.

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AUSTIN, A. D. & ALLEN, G. R. (1989) Parasitoids of *Uraba lugens* Walker (Lepidoptera: Noctuidae), with description of two new species of Braconidae. *Trans. R. Soc. S. Aust.* 113(4), 169-184, 30 November, 1989.

Information is presented on the large complex of hymenopteran and dipteran parasitoids associated with *Uraba lugens* Walker (the gumleaf skeletonizer) in South Australia. A key to the 22 species involved is presented, along with notes on identification and relationships with their host. Two species of microgastrine braconids are described, *Cotesia urabae* sp. nov. and *Dolichogenides eucalypti* sp. nov.; both are parasitoids of the larval stages of *U. lugens*.

KEY WORDS: *Uraba lugens*, Noctuidae, parasitoids, hyperparasitoids, Braconidae, Ichneumonidae, Aphelinidae, Chalcididae, Elasmidae, Eulophidae, Eurytomidae, Eupelmidae, Trichogrammatidae, Tachinidae.

Introduction

Uraba lugens Walker, the gumleaf skeletonizer, is a native noctuid moth and has been collected from all states of Australia (Turner 1944). It has been recorded as damaging stands of eucalypt species in eastern Australia (Brimblecombe 1962; Campbell 1962; Harris 1972¹, 1974; Harris *et al.* 1977²), the Adelaide region and south-western Western Australia (pers. comm. F. D. Morgan; Strelein 1988). Occasionally outbreaks of this species can defoliate large areas of native forests. Several such outbreaks have occurred in stands of *Eucalyptus camaldulensis* Dehnh. along the Murray Valley region of N.S.W. and Victoria, where, on at least four occasions, more than 30,000 ha have been affected (e.g. Campbell 1962; Harris 1974; Harris *et al.* 1977²). Apart from the widespread damage associated with this species, it is also responsible for the partial defoliation of individual eucalypt trees planted as ornamentals in parks and gardens.

Other than the work of the above authors and those of Morgan & Cobbinah (1977) and Cobbinah (1983), very little has been published on the biology and ecology of *U. lugens*, while even less has been reported on its parasitoids. Brimblecombe (1962) reported five species of primary parasitoids as

attacking *U. lugens* and Campbell (1962) ten species. However, in most cases these parasitoids were not identified further than family level and, if so, their identification was not reliable. One of us (G.R.A.) has recently completed a major study on the interaction of this insect and its parasitoids in the Adelaide region. This work shows that the immature stages of *U. lugens* support a diverse complex of hymenopteran and dipteran parasitoids (22 species — Table 1), which includes both primary parasitoids and hyperparasitoids. In this paper we provide a taxonomic framework for the information on the behaviour and ecology of this parasitoid complex and its interaction with *U. lugens*, which will be published elsewhere by G.R.A. Here we present a key to identify all the parasitoid species involved, and provide notes on their taxonomic position and biology, including information on the stage attacked and place of pupation. Two of the more common species reared from *U. lugens* larvae, which are members of the braconid subfamily Microgastrinae, and are the subject of detailed behavioural studies by G.R.A., are described here as new.

Materials and Methods

¹Harris, J. A. (1972) The effect of flooding on population density of the gum leaf skeletonizer moth, *Uraba lugens* Walk., in Barmah State Forest. Forest Commission, Victoria, Research Branch Report, No. 25 (unpubl.)
²Harris, J. A., Neumann, F. G. & Ward, B. (1977) An outbreak of the gum leaf skeletonizer, *Uraba lugens* Walker, in river red gum forest near Barmah. Forest Commission, Victoria, Research Branch Report, No. 87 (unpubl.).

All life history stages of *U. lugens* were collected from eucalypts (mostly *E. camaldulensis*, *E. leucoxylon* F. Muell. and *E. microcarpa* (Maiden) Maiden) between 1985 and 1988 at several sites within 7 km of Adelaide G.P.O. They were brought to the laboratory, held at 20°C in rearing cages, and larvae provided with new foliage, so that any parasitoids present could develop and emerge normally. Parasitoid cocoons found with their dead host in the field were also collected and reared in the laboratory at 20°C until adults emerged.

TABLE 1. Summary of relationships between *U. lugens* and its parasitoids and hyperparasitoids

Parasitoid species	Family	Primary (P) or Hyperparasitoid (H) Solitary (S) or Gregarious (G)	<i>U. lugens</i> stage attacked	Stage emerges from
<i>Trichogramma</i> sp.	Trichogrammatidae	P,S	egg	egg
<i>Coleophora uruhae</i>	Braconidae	P,S	larva	larva
<i>Dolichogenidea eucalypti</i>	Braconidae	P,S	larva	larva
<i>Euplectrus</i> sp.	Eulophidae	P,S	larva	larva
<i>Casinaria maura</i>	Ichneumonidae	P,S	larva	larva
<i>Exorista flaviceps</i>	Tachinidae	P,S	larva	larva
<i>Eriborus</i> sp.	Ichneumonidae	P,S	larva	pupa
<i>Xanthopimpla rhopaloceras</i>	Ichneumonidae	P,S	pupa?	pupa
<i>Antrocephalus</i> sp.	Coccidae	P,S	pupa	pupa
<i>Brachymeria</i> sp. 1	Chalcididae	P,S	pupa	pupa
<i>Wintheimia lateralis</i>	Tachinidae	P,S	?	pupa?
<i>Eurytoma</i> sp.	Eulophidae	P,G,H,S	pupa—	pupa/parasitoid cocoon
<i>Centriderus</i> sp.	Aphelinidae	H,G	—	parasitoid cocoon
<i>Bruchomeria</i> sp. 2	Chalcididae	H,S	—	parasitoid cocoon
<i>Elasmus australensis</i> species indet.	Elasmidae	H,G	—	parasitoid cocoon
<i>Polybius</i> sp. species indet.	Eulophidae	H,G	—	parasitoid cocoon
<i>Anastatus</i> sp.	Eupelmidae	H,S	—	parasitoid cocoon
<i>Mesochorus</i> sp.	Ichneumonidae	H,S	—	parasitoid cocoon
<i>Paraphylax</i> sp.	Ichneumonidae	H,S	—	parasitoid cocoon
<i>Pteromalus</i> sp.	Pteromalidae	H,S	—	parasitoid cocoon

Parasitoids were stored in a freezer or in 70% ethanol prior to mounting on pins or card points.

Material for S.E.M. study was washed in half strength concentrated liquid soap, rinsed in distilled water, dehydrated in an alcohol series and critical-point dried using an Emscope CPD 750, before being examined under a Cambridge Stereoscan 250 (Mk 3B) electron microscope. Terminology for morphology follows Bouček (1988), Eady (1968), Gauld (1984), Harris (1979), Mason (1986) and van Achterberg (1979). The term 'alitrunk' is used for the thorax plus propodeum, and 'gaster' is used for the post-propodeal segments. The abbreviation 'T' refers to the gastral tergites. Abbreviations for collections are: ANIC, Australian National Insect Collection, CSIRO, Canberra; WARL, Waite Agricultural Research Institute, Adelaide. Voucher specimens of all species are lodged in the Waite Institute collection.

Key to the parasitoids of *Uraba lugens* in South Australia

- Two pairs of wings developed; dorsal surface very rarely with stout bristles; wasp-like in appearance (ovi positor always developed in female and usually clearly visible (Figs 5, 7, 29)) (Hymenoptera). 2
Only one pair of wings developed (fore wings); dorsal surface with numerous stout bristles; blowfly like in appearance (Figs 48, 49) (scutum with several black longitudinal bands) (Tachinidae). 21
- Fore wing with relatively complete venation (e.g. Figs 1, 2, 6, 19). 3
Fore wing with pigmented venation reduced to anterior margin (e.g. Figs 21, 23, 27, 39). 9
- Fore wing with venation distal to pterostigma wanting (Figs 1, 2); vein 2m+cu absent (Braconidae). 4
Fore wing with distal veins present and well pigmented; vein 2m+cu present (Figs 4, 20) (Ichneumonidae). 5
- Propodeum with longitudinal medial carina, coarsely sculptured at least anteriorly (Fig. 12); legs red to red-yellow. *Cotesia uruhae* sp. nov.
Propodeum with large carinate areola and horizontal carinae extending to lateral margins of propodeum (Fig. 13); legs dark brown to black with distal parts reddish. *Dolichogenidea eucalypti* sp. nov.
- Fore wing with an areolet (Figs 4, 6). 6
Fore wing without an areolet (Figs 19, 20). 7
- Scutum and propodeum coarsely punctate or rugulose; ovipositor very short (Fig. 5); ♂ genitalia without long rods protruding posteriorly (body dark brown to black, legs reddish). *Casinaria maura* terman & Gauld
Scutum and propodeum generally unsculptured (except for propodeal carinae); ovipositor extending well past posterior gaster (Fig. 7); ♂ genitalia with pair of long rods (gonosquama) protruding posteriorly (body yellow-brown with darker markings). *Mesochorus* sp.
- Body bright yellow with black markings; T1 short and broad basally (Fig. 16). *Xanthopimpla rhopaloceras* Krieger
Body not so coloured; T1 narrow basally (Figs 17, 18). 8
- Fore wing with radial cell short and broad (Fig. 19); T1 flat, broadening distally (Fig. 17) (small species, length 2.3–3.2 mm not including ♀ ovipositor); body black-except for T2 which is yellow-brown. *Paraphylax* sp.
Fore wing with radial cell long and narrow (Fig. 20); T1 tubular in basal half, bulbous in distal half (Fig. 18) (large species, length 6.5–8.7 mm not including ovipositor for ♀; head and alitrunk black, gaster reddish-brown). *Eriborus* sp.

9. Femur of hind leg greatly expanded, toothed or serrated along lower margin (Fig. 24) (Chalcidae) 10
 Femur of hind leg normal, smooth along lower margin (Figs 25, 35) 12
10. Fore wing with marginal vein much longer than postmarginal vein (Fig. 22); apex of hind tibia tapering into strong spine (*Brachymeria*) 11
 Fore wing with marginal vein about same length as postmarginal vein (Fig. 21); apex of hind tibia perpendicularly truncate (Fig. 24) (large species, 4.8 mm in length; body black, hind leg dark red-brown marked with black) *Antrocephalus* sp.
11. Body black with red hind femur and tibia; 4.2–4.4 mm in length *Brachymeria* sp. 1
 Body black with white-yellow markings on regular and legs; 1.8–2.3 mm in length *Brachymeria* sp. 2
12. Hind coxa developed as large flat disc; hind tibia with distinct criss-cross pattern of setae (Fig. 25) (fore wing with stigmal vein very short (Fig. 23); body dark, tegula and legs except for hind coxa pale; body length of ♀ 1.8–2.7 mm, ♂ 1.3–1.9 mm) (Elastinidae)
Elasmus australiensis Girault
 Hind coxa, hind tibia and stigmal vein not as above 13
13. Pronotum (seen dorsally) large and quadrangular; dorsal surface of alitrunk coarsely sculptured (Fig. 26); fore wing venation as in Fig. 27 (body black and non-metallic, legs with some pale markings) (Eurytomidae) *Eurytoma* sp.
 Pronotum not large and quadrangular and alitrunk without such sculpturing; body often metallic in colour 14
14. Body length greater than about 1.5 mm; gaster separated from alitrunk by narrow waist (Figs 28, 29)
 Body length less than 1.0 mm (minute species); gaster broadly attached to alitrunk or appearing so (Fig. 44) 20
15. Tarsi 5-segmented (cf. Figs 24, 25) 16
 Tarsi 4-segmented (Fig. 35) 18
16. Mesopleuron not enlarged and shield-like (Fig. 28); body rather robust with large head and alitrunk (♀ gaster in lateral view sharply angled; ♂ gaster small and flattened; body length of ♀ 2.3–3.3 mm, ♂ 1.7–2.4 mm; metallic green in colour with yellow-brown legs and antennae) (Pteromalidae)
Pteromalus sp.
 Mesopleuron large and shield-like; body somewhat elongate (Fig. 29) (Eupelmidae). 17
17. Dorsal surface of scutum flattened with raised anterior triangular area (Fig. 31); fore wing with broad pigmented bands (Fig. 30) (mostly dark in colour with metallic green tinge; body 2.1–2.5 mm in length)
Anastatus sp.
 Dorsal surface of scutum not particularly flattened, without anterior raised area (Fig. 32); fore wings hyaline (head and alitrunk bright metallic green, gaster darker). gen. & species indet. (♂ only)
18. Fore wing with stigmal and postmarginal veins very short (Fig. 34); anterior scutellum longitudinally striate (Fig. 33) (body dark with metallic green tinge, 1.1–1.5 mm in length). *Pediobius* sp.
 Fore wing with stigmal and postmarginal veins long (Fig. 37); scutellum smooth or with fine reticulate sculpturing 19
19. Dorsal head and alitrunk with scattered long bristle-like hairs (Fig. 36) (body mostly dark and non-metallic; eyes red; antennae, legs and broad patch on dorsal gaster yellow-brown). *Euplectrus* sp.
 Dorsal head and alitrunk with shorter finer hairs (dorsal alitrunk with distinctive metallic green and yellow markings (Fig. 38)). gen. & species indet
20. Farsi 3-segmented (Fig. 40); antennae 5-segmented (Figs 41, 42); fore wing very broad (Fig. 39) (Trichogrammatidae) *Trichogramma* sp.
 Farsi 5-segmented (Fig. 47); antennae 6-segmented (Figs 45, 46); fore wing narrower (Fig. 43) (Aphelinidae) *Centradona* sp.
21. Hairs covering occiput (posterior part of head) silver-grey; abdomen in dorsal view with anterior, medial and posterior parts black, lateral areas brown (Fig. 48) *Wirthemia lateralis* (Macquart)
 Hairs covering occiput golden brown, 1st segment of abdomen black, other segments black with patches of silver (Fig. 49). *Exorista flaviceps* Macquart

Treatment of species**HYMENOPTERA**

Family Braconidae

Cotesia urabae sp. nov.

FIGS 2, 8, 10–12, 14

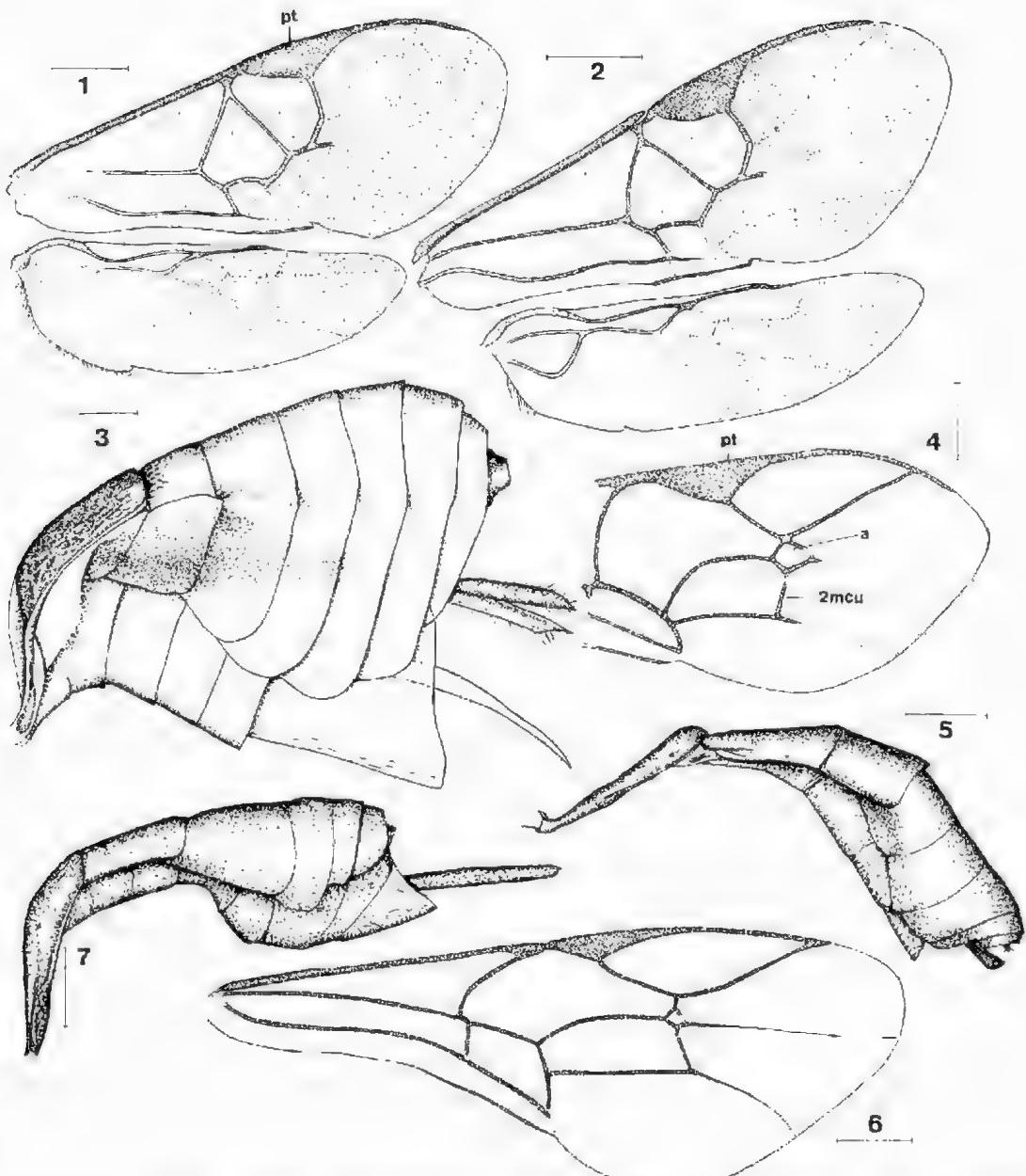
Holotype: ♀, ANIC, S. Aust., Adelaide (Mitcham), reared ex *Uraba lugens* on *Eucalyptus microcarpa*, coll. 14.v.1985, emerged 3.xi.1985, G. R. Allen. Paratypes: 8♀ ♀, 20♂ ♂, same data as holotype except some with different suburbs of Adelaide and different dates; 17♀ ♀, 13♂ ♂, S. Aust., Adelaide (Waite Institute campus), various collecting and emergence dates during 1964, L. Hope; 5♀ ♀, 1♂ ♂, S. Aust., National Park, Belair, coll. 20.xi.1964, emerged 25.xi.1964, F.D.M. (5♀ ♀, 5♂ ♂, ANIC; rest of material including 1♀ gold coated for SEM (wings slide-mounted) in WAR.).

Female

Length, 2.9 mm (2.5–3.2 mm, $n = 10$) including ovipositor.

Colour: Body black; palps yellow; legs except for coxa yellow-brown; hind leg infuscate distally, distal end of hind tibia with dark patch; anterior pleural-sternal region of gaster dark red; wings hyaline, stigma evenly and darkly pigmented, as is rest of fore wing venation.

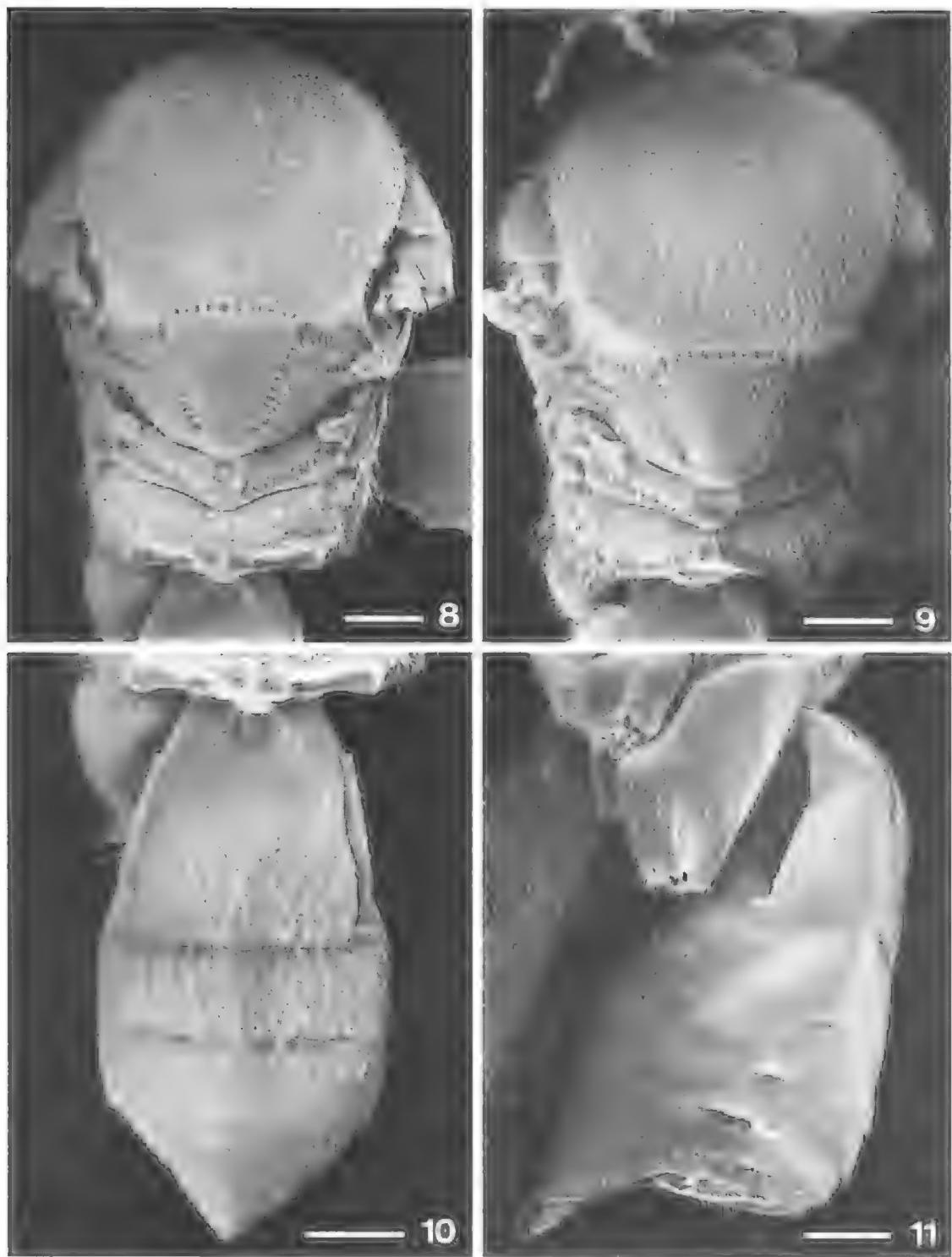
Head. In anterior view vertex arched so that head is somewhat circular; face and gena with longish white hairs and associated fine colliculate sculpturing; inner margins of eyes virtually parallel; in dorsal view ocelli in wide triangle, posterior tangent of median ocellus coincident with imaginary line across the anterior margins of lateral ocelli; frons and medial occiput smooth and hairless; temples with white hairs and associated colliculate sculpturing.



Figs 1-7. 1-2, Fore and hind wings: 1, *Dolichogenidea eucalypti* sp. nov., ♀; 2, *Coresia urabae* sp. nov., ♀; 3, Lateral view of gaster of *Dolichogenidea eucalypti* sp. nov., ♀; 4, Distal fore wing of *Mesochorus* sp., ♀; 5-6, *Cusinaria miera* Jerman & Gauld., ♀; 5, Lateral view of gaster; 6, Forewing; 7, Lateral view of gaster of *Mesochorus* sp., ♀. Scales: Figs 1, 2, 4 and 6 = 0.5 mm; Fig. 3 = 200 µm; Figs 5 and 7 = 1.5 mm. Abbreviations: a = areolet; pt = pterostigma.

turing which is slightly coarser than on face; vertex with few scattered short hairs otherwise smooth; antennae slightly longer than body, distal 4-5 segments only slightly longer than wide.
Alitrunk. Scutum punctate with covering of shortish hairs, punctuation denser along courses of notauli

and along lateral margins (Fig. 8), punctuation along posterior margin becoming slightly longitudinally elongate; courses of notauli faintly depressed, these faint depressions broadening posteriorly; scutellum faintly punctate; phragma of scutellum exposed along posterolateral margins (Fig. 8); propodeum



Figs 8-11. 8-9, Dorsal view of alitrunk: 8, *Cotesia urabae* sp. nov., ♀; 9, *Dolichogenidea eucalypti* sp. nov., ♀; 10-11, *Cotesia urabae* sp. nov., ♀; 10, Dorsal view of gaster; 11, Lateral view of gaster. Scales: = 200 µm.

coarsely rugose to rugose-striate in anterior half, generally smooth with faint rugose punctuation in posterior half; medial longitudinal carina well developed with associated short horizontal and oblique carinae (Fig. 12); mesopleuron finely punctate in anterior half with associated short hairs, smooth and hairless in posterior half except for compact group of 5–6 foveae medially; metapleuron smooth anteriorly, rugose-punctate posteriorly (Fig. 14); hind coxa faintly punctate on dorsal surface with associated short hairs, this sculpturing becoming coarser on ventral surface.

Wings. Fore wing with veins r and 2-SR sharply angled, r slightly longer than 2-SR; cu-a almost striate; distal part of basal cell and anterior part of sub-basal cell devoid of hairs or almost so; discal cell sparsely covered with hairs; hind wing with vein r (spectral) present (Fig. 2).

Gaster. T1 as wide as long, broadening posteriorly, surface in posterior two-thirds coarsely punctate to rugose-punctate, becoming coarsely striate in posterior one-quarter (Fig. 10); sclerotized part of T2 rectangular, slightly wider than T1, coarsely rugose-punctate with a few longitudinal striations, sculpturing fading to nearly smooth in postero-lateral corners, longitudinal midline smooth; T3 usually rugose-punctate in anterior one-quarter to two-thirds, with scattered hairs, posterior part smooth, in some specimens T3 virtually smooth throughout but always with at least anterior margin with band of punctuation; rest of tergites smooth with scattered hairs; in lateral view hypopygium pointed, extending past posterior gaster, with scattered fine hairs, ventroapical margin not indented (Fig. 11); ovipositor sheaths with few apical hairs.

Male

As for female except for length, 2.8 mm (2.6–3.1 mm, $n = 10$) and sexual differences (genitalia and development of hypopygium).

Other material examined: S. Aust., suburbs of Adelaide, various dates and collectors, 10♀, 16♂, 1♂ -WARI (excluded from type series because material is damaged or inadequately labelled).

Comments: The sculpturing on the propodeum and T1–T3, the shape of these sclerites, the form of the hypopygium and ovipositor, clearly place this species in *Cotesia Cameron*. *Cotesia* has previously been referred to as the *glomeratus* species-group of *Apanteles* s.l. (see Mason 1981; Nixon 1965), and is the largest generic level taxon in the subfamily Microgastrinae, the latter comprising some 1300–1500 described species world-wide (Mason 1981). In Australia *Cotesia* is common and diverse, but other than several species introduced from Europe

and North America as bio-control agents for certain lepidopteran pests (viz. *C. flavipes* Cameron, *C. glomerata* (L.) *C. kuzak* (Telenga), *C. marginiventris* (Cresson), *C. plutellae* (Kurdjumov), *C. rubecula* (Marshall) and *C. ruficrus* (Haliday)), the Australian fauna remains unstudied. A few poorly characterized species, which presently remain under the name *Apanteles* s.l., may turn out to belong in *Cotesia*. These species are unlikely to be conspecific with the present species as their type localities are outside the known distribution of *C. urubae* sp. nov. or they are associated with other hosts. There are no workable keys to Indo-Australian species of *Cotesia*. However, the key in Nixon (1974) to the north-western European fauna can be used to separate *C. urubae* sp. nov. from four of the seven introduced species mentioned above. Of the other three species, *C. flavipes*, is very different to *C. urubae* sp. nov. in that its body is strongly flattened dorsoventrally (see Austin 1989), while *C. kuzak* and *C. marginiventris* can only be identified reliably in association with their hosts, *Helicoverpa* spp. and *Mythimna connecta* (Walker), respectively.

Biology: *C. urubae* sp. nov. is a solitary, primary endoparasitoid and oviposits into early to intermediate larval instars of its host, emerging from intermediate to late instars before pupating. The pupal cocoon is alongside the host and is sulphur yellow-green with a surrounding silk matrix. This species has only been reared from *U. lugens*.

Dolichogenidea eucalypti sp. nov.

FIGS 1, 3, 9, 13, 15

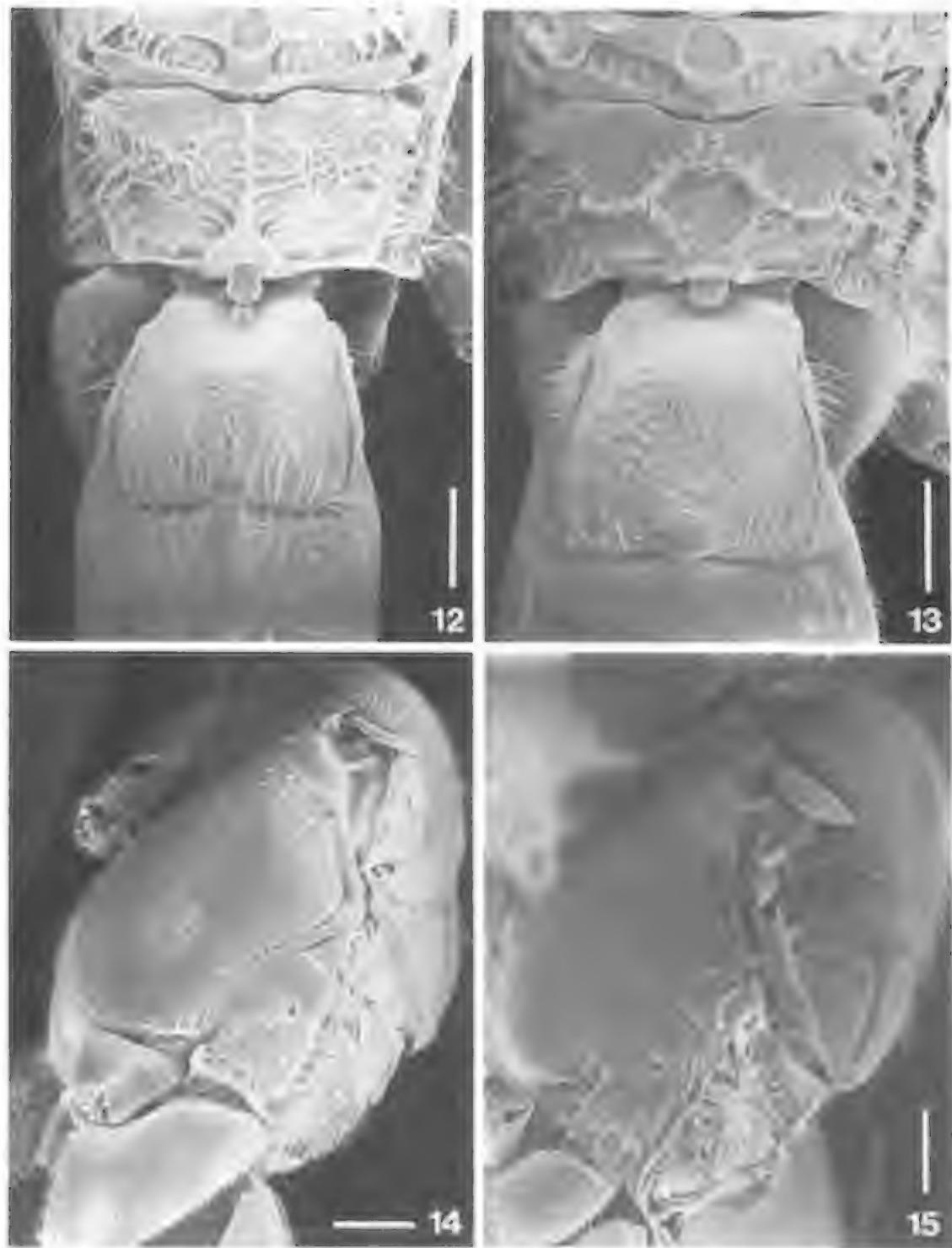
Holotype: ♀, ANIC, S. Aust., Adelaide (Highgate), reared ex *Uraba lugens* on *Eucalyptus camaldulensis*, collected 1.xi.1985, emerged 17.xi.1985. G. R. Allen. Paratypes: 15♀, 20♂ same data as holotype except some with different suburbs of Adelaide and different dates; 13♀, 5♂, S. Aust., Adelaide (Waite Institute campus), various collecting and emergence dates during 1964, L. Hope (5♀, 5♂), ANIC; rest of material including 1♀ gold coated for SEM (wings slide-mounted) in WARD.

Female

Length: 2.9 mm (2.5–3.1 mm, $n = 10$) including ovipositor.

Colour: Body black, wings hyaline with darkly pigmented venation, palps brown, legs black with distal fore legs, tarsi of mid and hind legs and tibio-femoral joint yellow-brown.

Head: Mostly smooth except for fine reticulate sculpturing associated with dense covering of short



Figs 12–15. 12–13, Propodeum and first and second tergites of gaster: 12, *Cotesia urabae* sp. nov., ♀; 13, *Dolichogenidea eucalypti* sp. nov., ♀; 14–15, Lateral view of alitrunk: 14, *Cotesia urabae* sp. nov., ♀; 15, *Dolichogenidea eucalypti* sp. nov., ♀. Scales: = 200 µm.

hairs; surface with characteristic dull lustre; in anterior view inner margins of eyes virtually parallel; in dorsal view ocelli forming wide triangle, posterior tangent of median ocellus coincident with imaginary line across the anterior margins of lateral ocelli; fine colliculate sculpturing and associated pilosity slightly denser across vertex and occiput, except for smooth narrow band around posterior margins of eyes; antennae reaching to posterior gaster or slightly beyond, distal three segments slightly longer than wide and sometimes slightly compressed.

Allitrunk. Scutum coarsely punctate with punctures mostly closer to each other than their own diameter, except along posterior border and along courses of notauli, which are thus faintly indicated (Fig. 9); scutellum smooth; scutum and scutellum densely covered with short hairs; melanotum rather broad, anterolateral margins emarginate so that phragma of scutellum well exposed; carinae forming propodeal areola raised well above surface, carinae extending laterally below horizontal midline, these carinae with dorsal and ventral extensions forming cristulae, but not enclosing spiracles (Fig. 13); anterior part of propodeum mostly smooth and setose, posterior part with faint rugose-punctate sculpturing which becomes more obvious laterally; mesopleuron setose in anterior half, smooth posteriorly; metapleuron mostly smooth, except for ventroposterior one-third which is rugose-punctate (Fig. 15); distal fore tarsus without spine opposed to tarsal claw.

Wings. Fore wing venation as in Fig. 1; costal and basal cells bare posteriorly; hind wing broad; vein $1\text{-}SC+R$ deeply bowed; r present but faint; cubitellian cell moderately broad; submediellian cell rounded posteriorly.

Gaster. T1 as wide as long, slightly widened in posterior half, lateral margins slightly emarginate, surface mostly punctate, striate-punctate along lateral margins and striate in posterolateral corners and along posterior margin (Fig. 13); sclerotized part of T2 slightly wider than T1, 2.5 x wider than long, mostly smooth with faint scattered punctures; T3 slightly longer than T2 (14:11); T4-T6 shorter than T2 (8:11); T7 very short, about one-quarter length of T2; T3-T6 all smooth; T2-T7 each with single transverse row of hairs; ovipositor and sheaths short, not extending far past posterior gaster; ovipositor with strong distal attenuation (Fig. 3); hypopygium lacking obvious lateral creases though weakened normally in ventral midline.

Male

As for female except as follows: Length 2.7 mm (2.5-2.8 mm, $n = 10$); allitrunk very slightly flattened dorsoventrally; fore wing stigma unpig-

mented in medial area so that it is transparent; rest of wing venation generally with less pigmentation than female; T1 sometimes with dense rugose-punctate sculpturing merging with posterior striations, otherwise same as female except for male genitalia and lacking hypopygium.

Comments: The sculpturing of the scutum and propodeum, shape of T1 and T2, form of the hypopygium, and shape and fringe of the vannal lobe of the hind wing clearly place this species in *Dolichogenidea* Viereck. Previously *Dolichogenidea* was considered as three related species-groups in the genus *Apanteles* s.l., viz. the *ultror*, *laevigatus* and *longipalpis* species-groups (see Mason 1981; Nixon 1965, 1967). This species falls into the *ultror* group which was revised by Nixon (1967) for the Indo-Australian region. In this work *D. eucalypti* sp. nov. keys out to *D. cleo* (Nixon) (couplet 23), a species known only from India and associated with a nymphalid host *Eriboae arja* Felder, or with some difficulty it keys as *D. caniae* (Wilkinson) (couplet 31), which is known only from Java and associated with a limacodid, *Cania bandura* Moore (Austin 1987). Apart from having different hosts, these species differ from *D. eucalypti* sp. nov. in that *D. caniae* has an unusual striate sculpturing pattern on T1 and T2, and *D. cleo* has the sub-basal cell evenly and darkly setose, the hind femur yellow in colour, the proximal half of the ovipositor very broad, and the mesopleuron coarsely rugose-punctate anteriorly. This is the fourth species of *Dolichogenidea* recorded from Australia, the others being *D. lipsis* (Nixon) comb. nov., *D. miris* (Nixon) comb. nov. and *D. tasmanica* (Cameron) comb. nov. Examination of the holotypes of these species shows that they differ from *D. eucalypti* sp. nov. in a number of important characters. All three have the ovipositor much longer, being at least as long as the hind tibia, and, in addition, *D. lipsis* and *D. tasmanica* have a white spot on the cheek and a much reduced propodeal areola. These species can be readily separated from *D. eucalypti* sp. nov. using the key in Nixon (1967).

Biology: *D. eucalypti* sp. nov. is a solitary, primary endoparasitoid which oviposits into early to intermediate larval instars of its host, emerging from intermediate to late instars before pupating. The pupal cocoon is spun alongside the host and is white in colour and lacks a surrounding silk matrix. This species has only been reared from *U. lugens*.

Familly Ichneumonidae
Xanthopimpla rhopalicera Krieger
 FIG. 16

This species is easily identified by its distinctive colour pattern and fore wing venation. In South Australia it is known from two specimens (WARI), one collected as an adult in the Adelaide region, the other reared from *U. lugens* at Keith. It is also known from Queensland and Tasmania where it has been recorded from *U. lugens*, and the tortriids *Epiphyas postvittana* (Walker) and *Merophyas divulsana* (Walker) (Brimblecombe 1962; Dumbleton 1940; Gauld 1984; also see Townes & Chui 1970). It is a solitary, primary endoparasitoid and emerges from the pupal stage of its host. See Gauld (1984) for additional taxonomic information and list of synonyms.

Paraphylax sp.
FIGS 17, 19

Paraphylax is a large Old World genus with more than 50 recognized species from Australia, the majority of which are undescribed (Gauld 1984). Where their biology is known *Paraphylax* spp. have been recorded as primary and hyperparasitoids, mostly of lepidopteran hosts. Apart from the characters given in the key this species is notable in comparison to other parasitoids associated with *U. lugens* for its relatively smooth unsculptured body (except for propodeal carinae) and lateral teeth on the propodeum. The species here belongs to the corvax species-group (see Gauld 1984) and is only known from the Adelaide region, where it has been reared as an obligate, solitary hyperparasitoid through *C. urabae* and *D. eucalypti*.

Eriborus sp.
FIGS 18, 20

This is a distinctive species when compared to the other Ichneumonids associated with *U. lugens*. In addition to the characters given in the key this species has distinctive reticulate-punctate sculpturing on the scutum, scutellum and propodeum. *Eriborus* sp. is a solitary primary parasitoid of *U. lugens*, ovipositing into the larval stages and emerging from the pupa. It is only known from the Adelaide region and has been reared from its host on various occasions since 1965 (WARI, unpublished records).

Cavimaria miera Jerman & Gauld
FIGS 5, 6

This species is a solitary, primary endoparasitoid easily recognized by its fore wing venation, short ovipositor and colour. It has been recorded from all states in Australia and, although it has been most commonly associated with *U. lugens*, *C. miera* has been reared from species belonging to three other

distantly related lepidopteran families — Geometridae, Oecophoridae, Notodontidae (see Gauld 1984; Jerman & Gauld 1988). The pupal cocoon is constructed near to (Jerman & Gauld 1988) or underneath (observations in this study) its dead larval host and is attached firmly to the leaf surface. It is grey-brown and marked with characteristic black spots. See Jerman & Gauld (1988) for additional taxonomic information and list of synonyms.

Mesochorus sp.
FIGS 4, 7

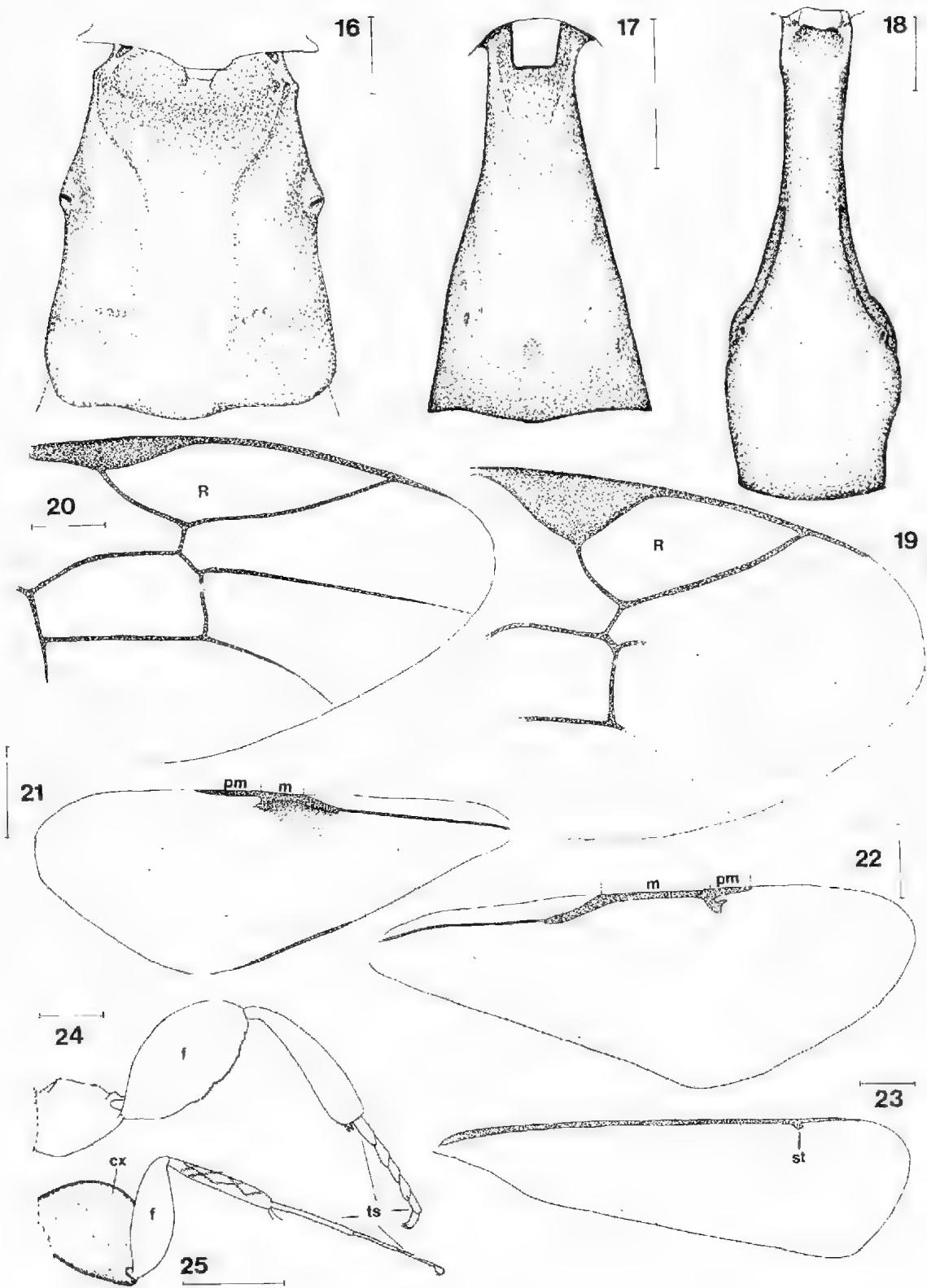
This is a large cosmopolitan genus of primary and hyperparasitoids of lepidopteran and coleopteran hosts; most Indo-Australian species are undescribed (Gauld 1984). The species recorded here is a solitary obligate hyperparasitoid of *U. lugens* through *C. miera*, *C. urabae* and *D. eucalypti*, and is known only from the Adelaide region. It is a pale coloured delicate species with fine thread-like antennae. The male is distinctive in having the gonosquama of the genitalia extending from the posterior gaster as a pair of long-tails.

Family Chalcididae
Brachymeria spp.
FIG. 22

This is a large genus in Australia with nearly 70 described species, the majority of which are primary, pupal parasitoids of Lepidoptera (Bouček 1988). The two species recorded here (both unidentified) can be separated easily by the characters in the key. Species 1 is a solitary, primary parasitoid of *U. lugens* and emerges from the host pupa. Species 2 is solitary and hyperparasitic through *C. urabae* and *D. eucalypti*, though it is not known whether this relationship is facultative or obligatory. In eastern Australia two species of *Brachymeria* have been reared from *U. lugens*, viz. *B. froggatti* (Cameron) (Brimblecombe 1962) and *B. ruhripius* Girault (Campbell 1962) (*B. ruhripius* is considered a junior synonym of *B. teuta* (Walker); see Bouček 1988). However, the material from these records would have been identified at a time when the Australian species in the genus were confused by most authors and hence might be misidentified. These names should thus be used with some care, especially since Bouček (1988) did not see any material in Australian collections or elsewhere reared from *U. lugens* that he could assign to either *B. froggatti* or *B. teuta*.

Antrocephalus sp.
FIGS 21, 24

This species is represented here by a single



specimen reared as a primary parasitoid from the pupa of *U. lugens* in the Adelaide region. It is easily distinguished by the characters in the key. There are more than 60 described Australian congeners which are discussed by Bouček (1988).

Family Eurytomidae

Eurytoma sp.
FIGS 26, 27

This is a large cosmopolitan genus with more than 60 described Australian species (Bouček 1988). Biologically the group is very diverse including phytophagous species, primary parasitoids (mostly of lepidopteran hosts) and hyperparasitoids. The species recorded here develops as either a primary gregarious parasitoid of *U. lugens*, or as a solitary hyperparasitoid through *C. urabae*.

Family Pteromalidae

Pteromalus sp.
FIG. 28

This species is relatively easily separated from other Chalcidoidea associated with *U. lugens* by its robust body and metallic green colour. The genus is taxonomically very complex and the Australian species are in need of revision (Bouček 1988). The species recorded here is an obligate, solitary hyperparasitoid reared from *U. lugens* through *C. micra*, *C. urabae* and *D. eucalypti* in the Adelaide region.

Family Encyrtidae

Elasmus australiensis Girault
FIGS 23, 25

A distinctive species recorded here as an obligate, solitary hyperparasitoid of *U. lugens* through *C. micra*, *C. urabae* and *D. eucalypti*. Previously it was known to be hyperparasitic and occasionally gregarious through an unknown ichneumonid associated with *U. lugens* in the A.C.T., and also has been collected from N.S.W., and northern and southern Qld (type locality: Gordonvale, Qld). This is the first record of *E. australiensis* from S. Aust., indicating that it is probably distributed throughout south-eastern Australia. See Riek (1967) for additional taxonomic information and list of synonyms.

Family Eulophidae

Euplectrus sp.
FIGS 36, 37

Euplectrus is a cosmopolitan genus of gregarious ectoparasitoids of lepidopteran larvae, which is represented in Australia by 13 described species (Bouček 1988). The species recorded here is solitary and only known from the Adelaide region. It attacks the early to intermediate larval stages, killing them before they pupate while pupating itself underneath the dead host.

Pediobius sp.
FIGS 33-35

This is a large, cosmopolitan genus of primary and hyperparasitoid species that attack a wide range of insect groups (Bouček 1988). There are more than 30 described Australian species, most of which do not have associated host information (Bouček 1988). The unidentified species recorded here is easily distinguished from other Hymenoptera associated with *U. lugens* by its distinctive venation and sculpturing on the scutellum. It is represented by four specimens (WARI) reared in the Adelaide region from *U. lugens* and developed as a solitary hyperparasitoid through *Euplectrus* sp. and as a gregarious hyperparasitoid through *D. eucalypti*.

Eulophidae (genus & species indet.)
FIG. 38

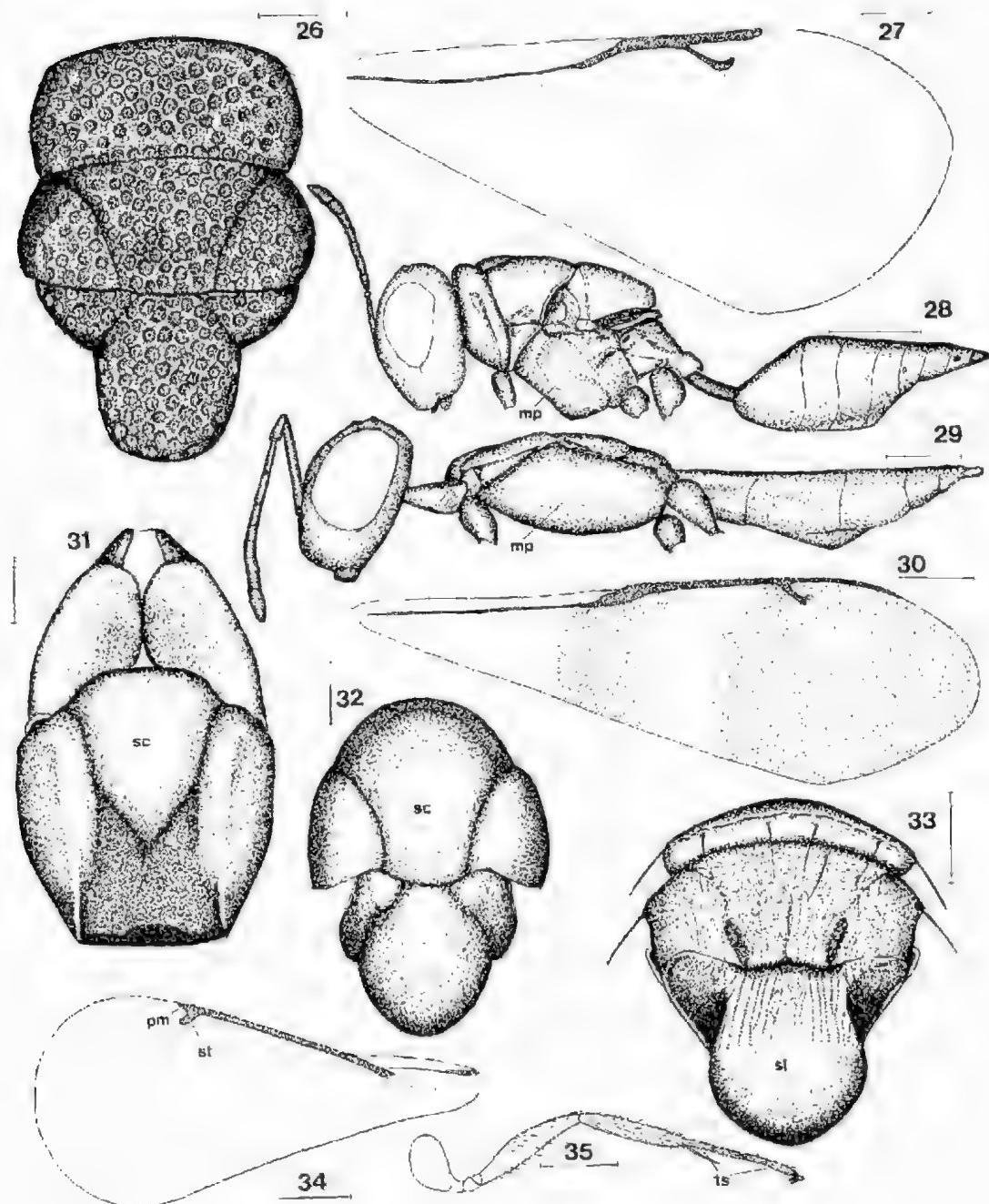
The two specimens reared as hyperparasitoids of *U. lugens* through *D. eucalypti* in the Adelaide region could not be identified to genus due to the poor condition of the material. They are different from the other eulophids recorded here and can be distinguished by the dorsoventrally flattened body and distinctive colour pattern.

Family Encyrtidae

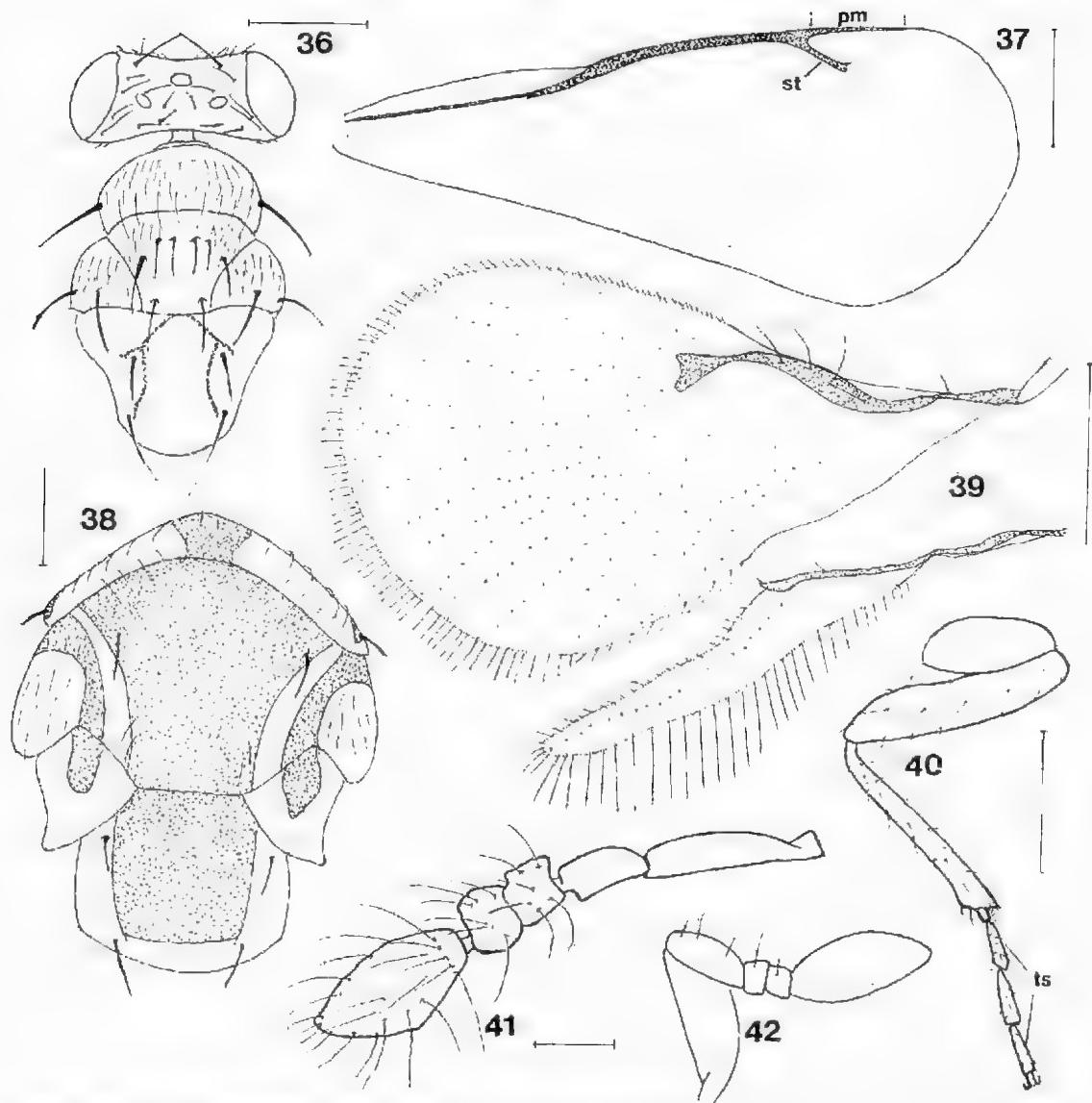
Anastatus sp.
FIGS 29-31

This species is easily separated from the other chalcidooids associated with *U. lugens* by its distinctive body shape and banded wings. The genus is cosmopolitan and known mainly as parasitoids of the eggs of Lepidoptera and Heteroptera,

Figs 16-25. 16-18. First tergite of gaster: 16, *Xanthopimpla rhopaloceras* Krieger, ♀; 17, *Paraphylax* sp., ♀; 18, *Eriborus* sp., ♀; 19-20, Distal fore wingst; 19, *Paraphylax* sp., ♀; 20, *Eriborus* sp., ♀; 21-23. Fore wings: 21, *Antrocephalus* sp., ♀; 22, *Brachymeria* sp. 2, ♀; 23, *Elasmus australiensis* Girault, ♀; 24-25. Hind legs: 24, *Antrocephalus* sp., ♀; 25, *Elasmus australiensis* Girault, ♀. Scales: Figs 16-19 = 250 µm; Figs 23 = 200 µm; Fig. 25 = 1.0 mm. Abbreviations: c = coxa; f = femur; m1 = marginal vein; pm = postmarginal vein; R = radial cell; st = stigmal vein; ts = tarsal segments.



Figs 26–35. 26–27, *Eurytoma* sp., ♀; 26, Dorsal view of alitrunk; 27, fore wing; 28–29, Lateral view of body; 28, *Pteromulus* sp., ♀; 29, *Anastatus* sp., ♀; 30, Fore wing of *Anastatus* sp., ♀; 31–33, Dorsal view of alitrunk; 31, *Anastatus* sp., ♂; 32, buprestidae genus & species indet., ♂; 33, *Pediobius* sp., ♀; 34, fore wing of *Pediobius* sp., ♀; 35, Hind leg of *Pediobius* sp., ♀. Scales. Figs 26, 27, 29, 34 and 35 = 250 µm; Fig. 28 = 0.5 mm; Fig. 30 = 200 µm; Figs 31–33 = 150 µm. Abbreviations: mp = mesopleuron; pm = postmarginal vein; sc = scutellum; sl = scutellum; st = stigmal vein; ts = tarsal segments.



Figs 36–42. 36–37, *Euplectrus* sp., ♀; 36, Dorsal view of head and alitrunk; 37, Fore wing; 38; Dorsal view of alitrunk of Euplectidae, genus & species indet., ♀ (stippling indicating colour pattern); 39–42, *Trichogramma* sp.; 39, Fore and hind wings, ♂; 40, Hind leg, ♀; 41, ♂ antenna; 42, ♀ antenna. Scales: Figs 36 and 37 = 250 µm; Figs 38 and 39 = 150 µm; Fig. 40 = 100 µm; Figs 41 and 42 = 50 µm (same scale line). Abbreviations: pm = postmarginal vein; st = stigmal vein; ts = tarsal segments.

although a few are recorded as hyperparasitoids through braconids. *Anastatus* is represented in Australia by 40 described species (Bouček 1988). The species recorded here is represented by three specimens reared as a gregarious hyperparasitoid through *C. urabae* and *D. eucalypti* in the Adelaide region.

Eupelmidae (genus & species indet.)
FIG. 32

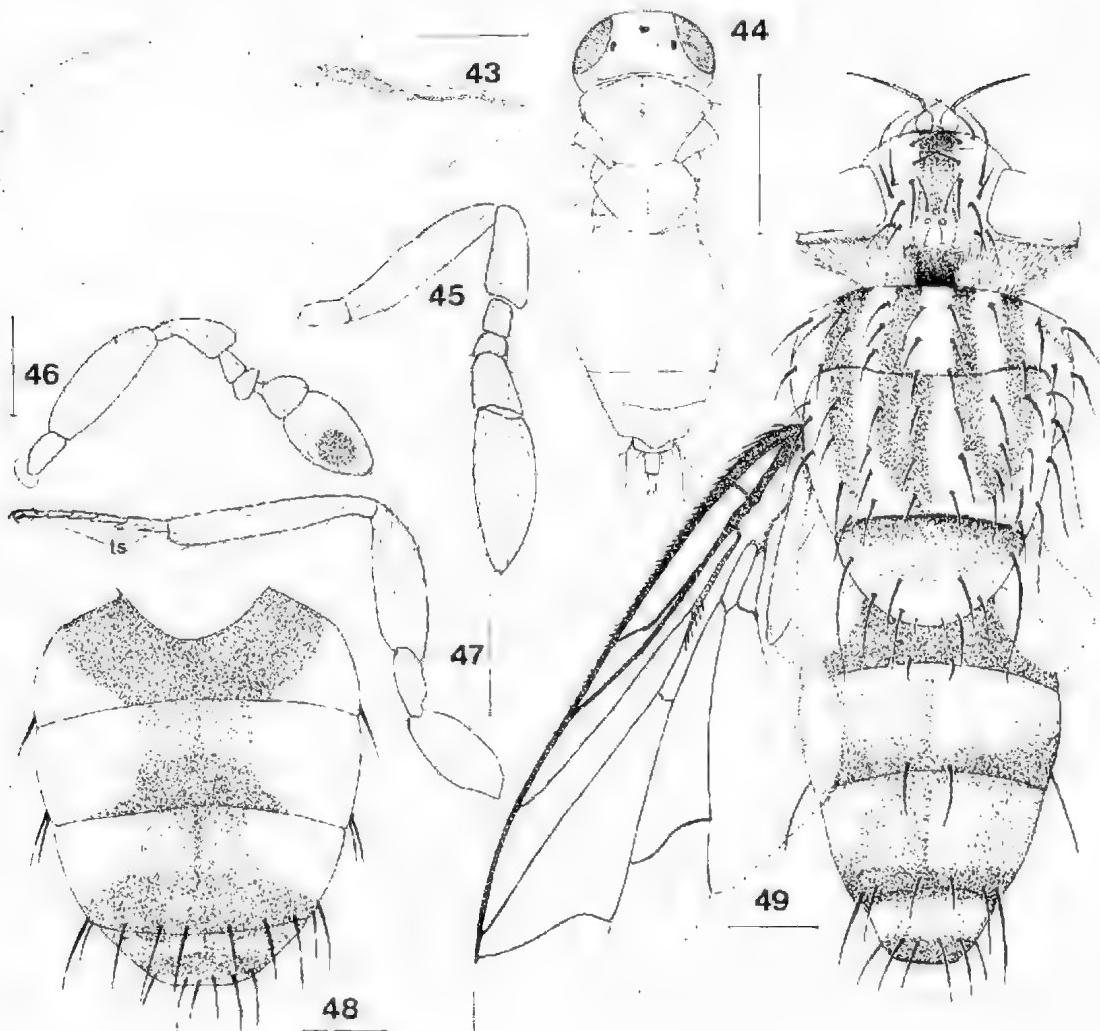
A single male specimen reared as a hyperparasitoid of *U. lugens* through *C. urabae* in the Adelaide region could not be identified to genus, but it is not *Anastatus* sp., from which it can be separated by the characters in the key.

Family Trichogrammatidae

Trichogramma sp.

FIGS 39–42

The members of this cosmopolitan genus are



Figs 43-49. 43-47, *Centrodora* sp.; 43, Fore wing, ♀; 44, Dorsal view of whole body, ♀; 45, ♂ antenna; 46, ♂ antenna; 47, Hind leg, ♀; 48, Abdomen of *Wlathemia lateralis*, ♀ (Macquart); 49, Dorsal view of *Foorista fluviceps* Macquart, ♂ (stippling showing colour pattern in Figures 46 and 47). Scales: Fig. 43 = 200 µm; Fig. 44 = 300 µm; Figs 45-47 = 50 µm (same scale line for Figs 45 and 46); Figs 48 and 49 = 1.0 mm. Abbreviation: ls = tarsal segments.

obligate, primary parasitoids of insect eggs, most frequently those of Lepidoptera. It is the only egg parasitoid of *U. lugens* so far recorded, and it can be identified by the characters in the key, as well as its minute size, distinctive fore wing venation, fore wing setal pattern, and very narrow hind wing. This species is a solitary parasitoid known only from the Adelaide region. We have not seen material of the *Trichogramma* sp. reared from *U. lugens* in the Murray Valley in N.S.W. (Campbell 1962), which may be the same species to that recorded here.

Family Aphelinidae

Centrodora sp. FIGS 43-47

This is a cosmopolitan genus of about 40 described species (Hayat 1983), most of which are primary parasitoids of the eggs of Orthoptera and Homoptera, although at least one species is reported to be hyperparasitic (Gordh 1979; also see Viggiani 1984). The species recorded here is an obligate, gregarious hyperparasitoid of *U. lugens*

through *C. urahae* or *D. eucalypti*. Apart from the characters in the key and the life history stage attacked, *Centrodora* sp. can be separated from the other parasitoids associated with *U. lugens* by its minute size, wing venation, and ovipositor which is more than half the length of the gaster (the ovipositor being significantly less than half the gastral length in *Trichogramma* sp.).

DIPTERA

Family Tachinidae

Wirthemia lateralis (Macquart)

FIG. 48

Previously this species has been collected at various localities in all states of Australia. It has been reared from host species belonging to seven lepidopteran families, viz. Arctiidae, Noctuidae, Pieridae, Notodontidae, Nymphalidae, Saturniidae and Geometridae. (Crosskey 1973; Cantrell 1986, 1989). The only record from *U. lugens* is from specimens in this study (3 specimens, Waite Institute campus, J. Cobbinah, 1975, WARI). *W. lateralis* oviposits onto the external surface of a host larva. After hatching the fly larva penetrates the host larva and usually emerges from the host pupa, although we were not able to confirm its biology in this study. See Crosskey (1973) and Cantrell (1986, 1989) for additional taxonomic information and list of synonyms.

Exorista flaviceps Macquart

FIG. 49

This species has been recorded from all states of Australia and the N.T. (Cantrell 1985), and has been reared from members of nine lepidopteran families, viz. Lymantriidae, Anthelidae, Pieridae, Agaric-

tidae, Sphingidae, Geometridae, Notodontidae, Lasiocampidae and Noctuidae (Crosskey 1973; Cantrell 1986). It oviposits onto the surface of *U. lugens* larvae. After hatching the fly larva burrows into the host to feed and develop internally, finally emerging from late larval instars to pupate outside the dead host. The colour pattern on the abdomen and occiput of the head is the easiest way to distinguish this species from *W. lateralis*. See Cantrell (1985) for additional taxonomic information and list of synonyms.

Other Parasitoids

From *U. lugens* in Queensland Brimblecombe (1962) reared two ichneumonoid species which have not been recorded in S. Aust., viz. *Irabutha* sp. (Ichneumonidae) and *Campyloneura* sp. (Braconidae). Also Gauld (1984) reports the following ichneumonids as having been reared from *U. lugens*: *Stromesostenus* spp., *Campoplex* sp. and *Pristomerus* sp., but again, they were not reared during this study and may not be found in S. Aust.

Acknowledgments

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**CONTRIBUTIONS TO THE TAXONOMY OF AUSTRALIAN
BUPRESTIDAE (COLEOPTERA): NEW SPECIES OF ASTRAEUS AND
STIGMODERA (CASTIARINA) AND A KEY TO ASTRAEUS (S.S.)**

*BY S. BARKER**

Summary

Astraeus meyricki Blackburn is resurrected from synonymy, redescribed and illustrated. *Astraeus badeni* van de Poll is redescribed and illustrated and the following five new species of *Astraeus* (*sensu stricto*) are described: *A. aridus* sp. nov., *A. occidentalis* sp. nov., *A. princeps* sp. nov., *A. williamsi* sp. nov., *A. yarrattensis* sp. nov. A revised key to *Astraeus* (s.s.) is provided. The egg of *A. pygmaeus* van de Poll is illustrated and some biological information given. Two new species of *Stigmodera* (*Castiarina*) are described: *S. garnettensis* sp. nov., *S. wellsae* sp. nov.; the first has sexually dimorphic colour pattern, rare in the sub-genus.

KEY WORDS: New species, *Astraeus*, *Stigmodera* (*Castiarina*), Coleoptera, Buprestidae.

CONTRIBUTIONS TO THE TAXONOMY OF AUSTRALIAN BUPRESTIDAE (COLEOPTERA): NEW SPECIES OF *ASTRAEUS* AND *STIGMODERA (CASTIARINA)* AND A KEY TO *ASTRAEUS* (s.s.)

by S. BARKER*

Summary

BARKER, S. (1989) Contributions to the taxonomy of Australian Buprestidae (Coleoptera): New species of *Astraeus* and *Stigmodera (Castiarina)* and a key to *Astraeus* (s.s.). *Trans. R. Soc. S. Aust.* 113(4), 185-194, 30 November, 1989.

Astraeus meyricki Blackburn is resurrected from synonymy, redescribed and illustrated. *Astraeus badeni* van de Poll is redescribed and illustrated and the following five new species of *Astraeus* (*sensu stricto*) are described: *A. aridus* sp. nov., *A. occidentalis* sp. nov., *A. princeps* sp. nov., *A. williamsi* sp. nov., *A. yarralensis* sp. nov. A revised key to *Astraeus* (s.s.) is provided. The egg of *A. pygmaeus* van de Poll is illustrated and some biological information given. Two new species of *Stigmodera (Castiarina)* are described: *S. garnettensis* sp. nov., *S. wellsi* sp. nov.; the first has sexually dimorphic colour pattern, rare in the sub-genus.

KEY WORDS: New species, *Astraeus*, *Stigmodera (Castiarina)*, Coleoptera, Buprestidae.

Introduction

The buprestid genus *Astraeus* was revised by Barker (1975) and additional species described by Barker (1977). No further information has been published. Fresh material has now come to hand and five new species are described herein including one species from the Flinders Ranges, S. Aust., which was misidentified in the revision of Barker (1975). The separate status of *A. badeni* van de Poll and *A. meyricki* Blackburn has been in doubt since they were described. A re-examination of the specimens available has convinced me that they are separate species. The key to *Astraeus* (s.s.) given by Barker (1975) requires updating to include three new species published by Barker (1977), five new species described herein and one species resurrected from synonymy. A new key is presented and new locality records of two species recorded. The egg of *A. pygmaeus* van de Poll is illustrated, the first such observation of an *Astraeus* species, together with biological information on *A. pygmaeus*. Two new species of *Stigmodera (Castiarina)* are described and illustrated; one being unusual in showing sexual dimorphism in colour pattern, a rare occurrence in this sub-genus.

Materials and Methods

Male genitalia were prepared and displayed by the method described by Barker (1987). Specimens for S.E.M. were dehydrated prior to being coated with gold-palladium. Abbreviations used in the text for museum and private collections following Wall

(1979) are: BMNH British Museum (Natural History), London; JHQA Mr J. Hasenpusch, Innisfail; MNHN Museum National d'Histoire Naturelle, Paris; NMVA Museums of Victoria, Melbourne; SAMA South Australian Museum, Adelaide; WAMA Western Australian Museum, Perth; GWNA Mr G. Williams, Landsdowne; GWQA Mr G. Wood, Atherton.

Resurrection of *Astraeus meyricki*.

Van de Poll (1892) considered *A. meyricki* Blackburn a synonym of *A. badeni* van de Poll but Blackburn (1895) disagreed. Barker (1975) followed van de Poll. I have re-examined the two male syntypes of *A. meyricki* held respectively in the BMNH and SAMA collections and compared them with specimens in the SAMA identified by comparison with the female holotype of *A. badeni* held by the MNHN. The pronotum of *A. badeni* is widest medially and differs from *A. meyricki* which is widest basally. Male genitalia of *A. meyricki* are broader than those of *A. badeni* and are rounded more abruptly at the apices (Figs 1C, 1E). I conclude that *A. meyricki* (Fig. 2B) is a good species and hereby resurrect it from the synonymy of *A. badeni* (Fig. 2A). Both species are redescribed here.

Astraeus (Astraeus) williamsi sp. nov. FIGS 1A, 2D

Holotype ♂, Peninsular Rd, Lansdowne, N.S.W., 10.x.1987, G. Williams, SAMA 12129.

Allotype ♀, same data as holotype, SAMA 12120.

Paratypes: N.S.W.: 5 ♂♂, Peninsular Rd,

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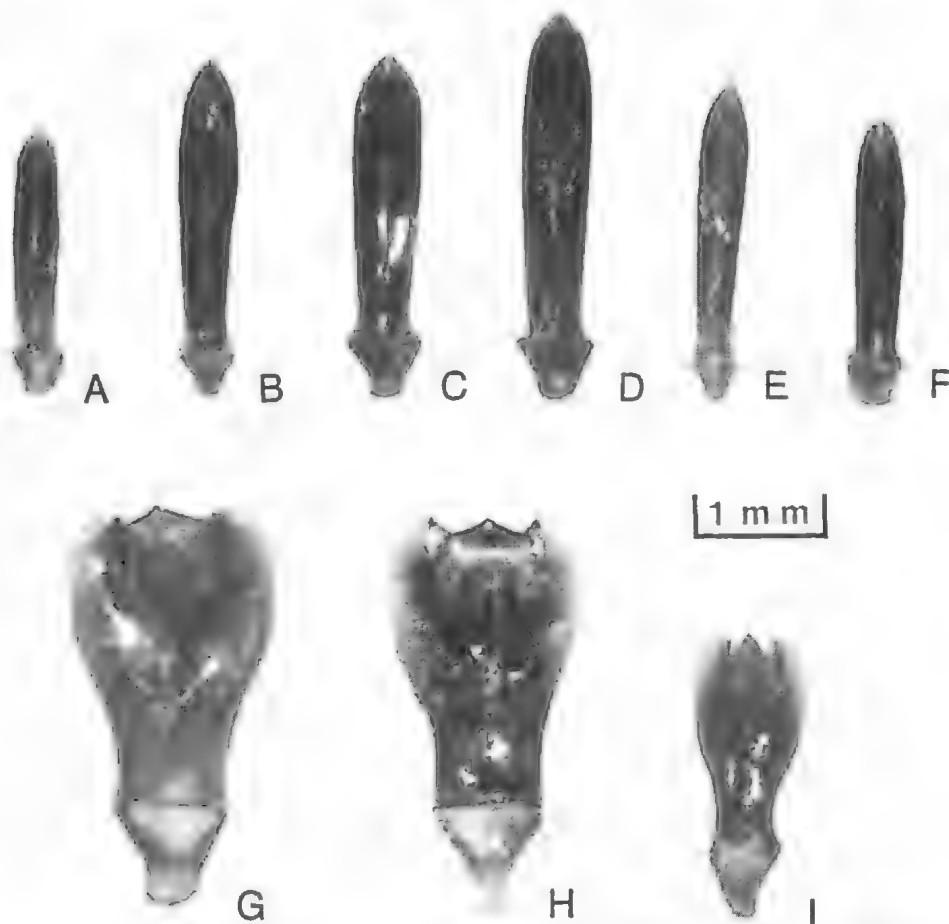


Fig. 1. Photomicrographs of male genitalia of the following *Astraeus* (*Astraeus*) species: A. *Astraeus williamsi* sp. nov., B. *A. aridus* sp. nov., C. *A. meyricki* Blackburn, D. *A. occidentalis* sp. nov., E. *A. badeni* van de Poll, F. *A. yarrattensis* sp. nov., and the following *Stigmodera* (*Castiarina*) species: G. *Stigmodera garnettensis* sp. nov., H. *S. vallisi* Deququet, I. *S. wellsae* sp. nov.

Lansdowne, 17.xi.1980, 23.x.1980, 30.x.1980, 22.x.1982, 28.x.1988, G. Williams, GWNA.

Colour: Head blue-green or blue. Antennae, segments: 1–3 coppery; 4–11 blue. Pronotum blue laterally, purple medially. Elytra dark blue, each elytron with following yellow markings: basal spot; pre-medial fascia represented by mark over humeral fold and spot near suture; post-medial fascia touching margin but not reaching suture; small pre-apical spot. Ventral surface dark blue. Legs: femora dark blue; tibiae mostly dark blue, distal tip testaceous; 1st tarsomere mostly testaceous, distal tip blue, 2nd tarsomere mostly testaceous, distal tip blue, 3–4 tarsomeres blue. Hairs silver.

Shape and sculpture. Head closely punctured, without median keel, hairy. Pronotum closely

punctured; laterally parallel-sided at base, rounded posteromedially to apex, hairy. Elytra costate, intervals flat and smooth each with basal row of punctures; laterally parallel-sided basally, rounded posteromedially and tapered to sharp marginal spine; sutural spine sharp, rounded inner margin, humeral fold moderately developed, angled (*vide* Barker 1975 Fig. 1E). Ventral surface shallowly punctured, moderately hairy, hairs short.

Size. Males, $7.5 \pm 0.18 \times 2.9 \pm 0.08$ mm (6). Females, 7.9×3.2 mm (2).

Male genitalia: (Fig. 1A). Parameres parallel-sided from basal piece, widened medially, tapered, rounded and tapered to apex. Apophysis of basal piece broad, rounded apically.

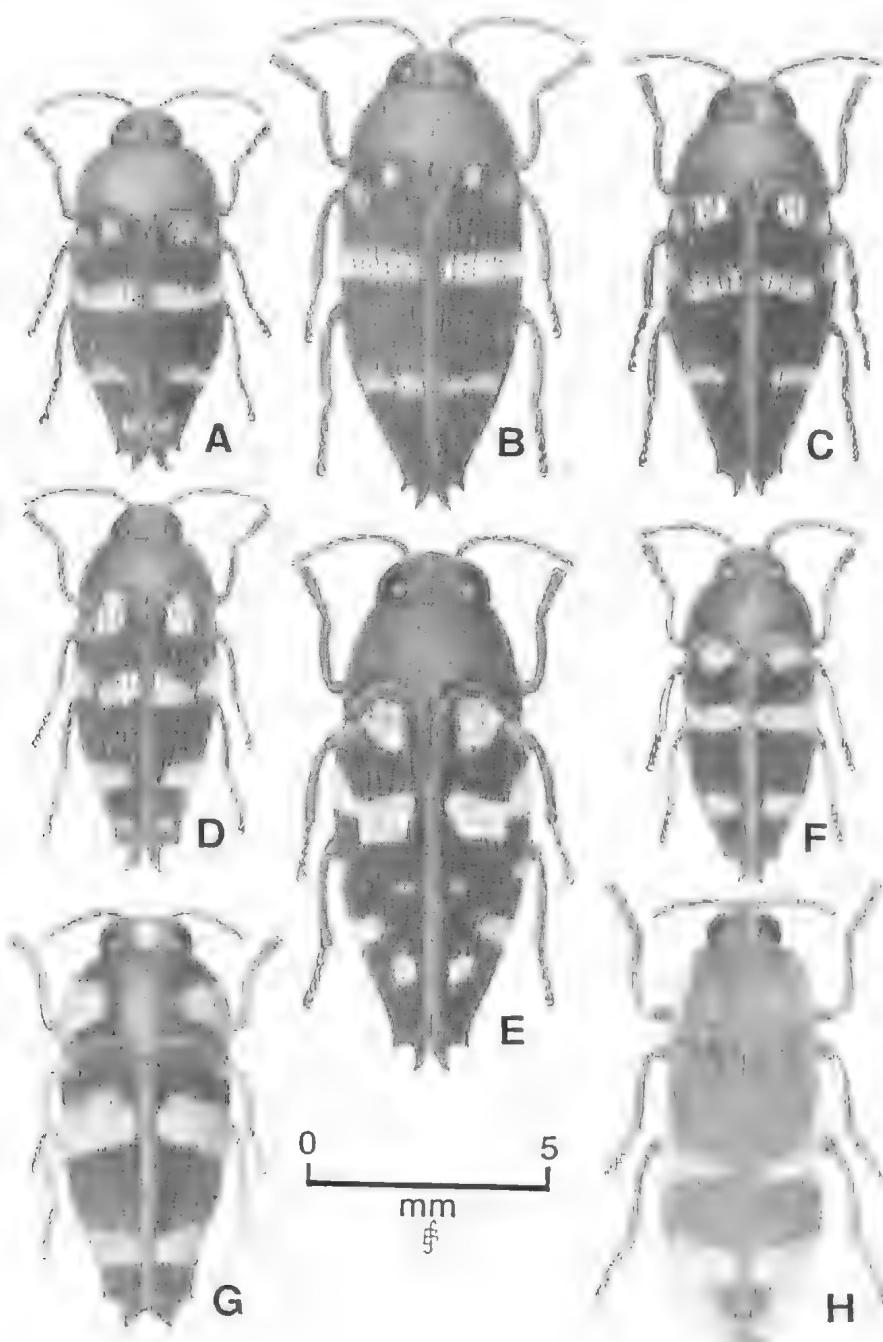


Fig. 2. Habitus illustrations of the following species: A. *Astraeus badeni* van de Poll, B. *A. meyricki* Blackburn, C. *A. aridus* sp. nov., D. *A. williamsi* sp. nov., E. *A. occidentalis* sp. nov., F. *A. yarrattensis* sp. nov., G. *A. princeps* sp. nov., H. *Stigmodera wellsae* sp. nov.

Remarks: Named after Mr G. Williams, Lansdowne.

Astraeus (Astraeus) yarrattensis sp. nov.
FIGS 1F, 2F

Holotype ♂, Yarratt State Forest, NE Wingham, N.S.W., 11.xi.1981, G. Williams, SAMA 1 21221.

Allotype: ♀, 10 km SSW Laurieton, N.S.W., 6.xi.1980, G. Williams, SAMA 1 21222.

Paratypes: N.S.W.: 1 ♂, same data as holotype, GWNA; 3 ♂♂, Yarratt State Forest, NE Wingham, 29.x.1981, 16.xi.1982, G. Williams, GWNA; 1 ♂, Bom Bom State Forest, SE Grafton, 14.vii.1984, G. Williams, GWNA; 1 ♀, Mitchells' Island, (Factory Rd), E Taree, 9.xi.1988, G. Williams, GWNA.

Colour. Male: Head blue-green, dark blue basally with purple reflections. Antennae, segments: 1–3 coppery; 4–11 blue. Pronotum dark blue with purple reflections, blue at lateral and basal margins. Female: Head and pronotum dark blue; rest as in male. Elytra dark blue with following yellow markings on each elytron: large basal spot; pre-medial fascia covering humeral fold but not reaching suture; post-medial fascia covering margin but not reaching suture. Ventral surface blue. Legs: femora blue; tibiae blue at proximal end, rest testaceous; 1st tarsomere testaceous; 2–4 tarsomeres blue. Hairs silver.

Shape and sculpture: Head closely punctured, glabrous median keel, hairy. Pronotum closely punctured; laterally parallel-sided basally, rounded posteromedially, tapered to apex; median impressed line from middle to apical margin, laterally hairy. Elytra costate, intervals flat, basally wrinkled, each with row of punctations; laterally tapered from base, rounded posteromedially, tapered to sharp marginal spine; sharp sutural spine, rounded inner margin; humeral fold well developed and angled. Ventral surface closely punctured, moderately hairy, hairs medium length.

Size: Males, 6.9 x 2.9 mm (6). Females, 7.4 x 3.1 mm (2).

Male genitalia: (Fig. 1F). Parameres angled outwards from basal piece, more or less parallel-sided, rounded to apex. Apophysis of basal piece broad, rounded apically.

Remarks: Named after the type locality.

Astraeus (Astraeus) aridus sp. nov.
FIGS 1B, 2C

Astraeus badeni: Barker 1975, p. 131.

Holotype ♂, Puttapa Gap, 21 km S Copley, S. Aust., Flinders Ranges, 21.x.1971, S. Barker, SAMA 1 21223.

Allotype: ♀, same data as holotype, SAMA 1 21224. *Paratypes*: S. Aust.: 6 ♂♂, 8 ♀♀, same data as holotype SAMA; 8 ♂♂, 6 ♀♀, Derna Pass, 25.x.1969, N. McFarland, SAMA.

Colour: Head, antennae, pronotum black with blue reflections. Elytra black with blue reflections and following yellow markings: basal spot; fascia covering humeral fold, not reaching suture, concave anteriorly, often represented by two spots; short post-medial fascia touching margin but not suture, concave posteriorly. Ventral surface and legs black with purple reflections. Hairs silver.

Shape and sculpture: Head closely punctured, no median keel, hairy. Pronotum closely punctured; laterally rounded and narrowed from base to apex; hairy. Elytra costate, intervals flat, each with row of punctures; laterally parallel-sided basally, rounded posteromedially to marginal spine; both spines sharp, sutural spine with rounded inner margin, humeral fold poorly developed, slightly angled. Ventral surface shallowly punctured, moderately hairy, hairs medium length.

Size: Males, 8.9 ± 0.10 x 3.5 ± 0.07 mm (15). Females, 9.1 ± 0.14 x 3.6 ± 0.07 mm (15).

Male genitalia: (Fig. 1B). Parameres angled outwards from basal piece, rounded anteromedially to apex. Apophysis of basal piece medium width, rounded apically.

Remarks: All specimens were collected on the leaves and stems of *Melaleuca glomerata* F. Muell. from the same locality. Derna Pass is a synonym of Puttapa Gap. The specific name is derived from *aridus* L., dry.

Astraeus (Astraeus) badeni van de Poll
FIGS 1E, 2A

Astraeus badeni van de Poll 1889: 84, 93, 94, pl. 2, figs 7, 7a, Blackburn 1891: 496; Kerremans 1892: 101; van de Poll 1892: 67; Blackburn 1895: 45, 46; Kerremans 1903: 148; Carter 1929: 282; Obenberger 1930: 365; Barker 1975: 131.

Astraeus badeni disjunctus Obenberger 1928: 204; 1930: 365; Barker 1975: 131

Astraeus mayrickeri Blackburn 1890: 1256, 1257; van de Poll 1892: 67; Kerremans 1892: 101; Kerremans 1903: 148; Carter 1929: 282; Obenberger 1930: 365; Barker 1975: 131.

Type: Holotype ♀, Gawler, MNHN.

Colour: Head, antennae, pronotum black with blue and purple reflections. Elytra black with purple reflections and following yellow markings on each elytron: basal spot; pre-medial fascia from margin over humeral callus, not reaching suture, concave anteriorly; short post-medial fascia from margin not reaching suture, concave posteriorly; small pre-apical spot. Ventral surface black with bronze and purple reflections. Legs black with blue and purple reflections. Hairs silver.

Shape and sculpture: Head closely punctured, no median keel, hairy. Pronotum closely punctured; laterally parallel-sided basally, rounded, indented to apex, hairy. Elytra costate, intervals flat each with row of punctures; laterally parallel-sided basally, rounded posteromedially, abruptly tapered to sharp marginal spine; sharp sutural spine, rounded inner margin, humeral fold moderately developed, angled. Ventral surface shallowly punctured, moderately hairy, hairs long.

Size: Males, 7.9 x 3.4 mm (6). Females, 8.4 x 3.6 mm (8).

Male genitalia: (Fig. 1E). Parameres angled outwards from basal piece for most of length, rounded to apex. Apophysis of basal piece medium width, rounded apically.

Distribution: S. Aust.: Gawler, Morgan, Murray Bridge, Nuriootpa, Vic.: Inglewood. W.A.: Marvel Loch, Southern Cross.

Remarks: *A. badeni* differs from congeners in the bulbous appearance of the pronotum and the more abruptly tapering apices of the elytra. It is a short broad species. A specimen in the SAMA collected by Tepper at Nuriootpa, S. Aust. has 'on *Callitris*' on the label, the only specimen seen with a recorded host plant.

Astraeus (Astraeus) meyericki Blackburn
FIGS 1C, 2B

Astraeus meyericki Blackburn, 1890: 1256, 1257; 1895: 45, 46

Type: Syntype ♂, no data, BMNH; syntype ♂, W. Australia, SAMA.

Colour: Head, antennae, pronotum black with purple reflections. Elytra black with following yellow marks on each elytron: small basal spot; pre-medial fascia covering humeral fold, not reaching

suture; post-medial fascia not reaching margin of suture. Ventral surface black with purple reflections. Legs dark brown with purple reflections. Hairs silver.

Shape and sculpture: Head closely punctured, shallow basal median sulcus, without median keel, hairy. Pronotum closely punctured, with prominent basal fovea, median glabrous line from base to middle; laterally rounded from base to apex. Elytra costate, intervals flat, each with row of punctures; laterally tapered from base, rounded posteromedially then tapered to sharp marginal spine; sharp sutural spine, rounded inner margin; humeral fold very poorly developed, very slightly angled. Ventral surface shallowly punctured, moderately hairy, hairs medium length.

Size: Male, 10.6 x 4.5 mm (2).

Male genitalia: (Fig. 1C). Parameres angled outwards from basal piece, rounded to apex. Apophysis of basal piece medium width, rounded apically.

Remarks: There is a female specimen lodged in the SAMA possibly belonging to this species which I identified as *A. badeni* (Barker 1975 p. 133). It was collected 18 km SW Three Springs, W.A., on *Dryandra cirisoides*, 8.xi.1968, N. McFarland.

Astraeus (Astraeus) princeps sp. nov
FIG. 2G

Holotype: ♀, Prince of Wales Island, Qld, Feb 1939; SAMA 121225.

Paratype: Qld: 1 ♀, same data as holotype SAMA.

Colour: Head black with blue reflections and yellow frontal spot. Antennae black with blue reflections. Pronotum black with blue reflections and large lateral yellow marks. Elytra black with blue reflections and following yellow marks on each elytron: broad pre-medial fascia covering margin but not reaching suture, obliquely angled anteriorly; broad post-medial fascia covering margin but not reaching suture. Ventral surface dark blue. Legs red brown. Hairs silver.

Shape and sculpture: Head shallowly punctured, no median keel, few short hairs. Pronotum shallowly punctured, laterally rounded from base to apex, widest medially, few short hairs. Elytra costate, intervals flat, each with row of punctures, surface wrinkled basally; laterally tapered from base, rounded posteromedially, tapered to sharp marginal

spine; sharp sutural spine, inner margin straight and turned upward, with extended marginal interval between spines; humeral fold absent. Ventral surface shallowly punctured, moderately hairy, hairs medium length.

Size: Females, 7.9 x 3.4 mm (2).

Remarks: Both specimens were given to Mr S. Watkins by Robert G. Wind, insect supply dealer and resident of Monterey, California. His Australian wife had been stationed on Prince of Wales Island prior to World War II and presumably she was the collector. They are unique to the sub-genus due to the coloration on the head and pronotum. The dorsal coloration may have been pink or red in life and now faded. The name is derived from *princeps* L., leader.

Astracus (Astracus) occidentalis sp. nov
FIGS 1D, 2E

Holotype: ♂, 99 km S Overland Roadhouse, Carnarvon Hwy, W.A., 25.ix.1980, on *Casuarina dieckiana*, S. Barker, SAMA, I 21226.

Allotype: ♀, same data as holotype; SAMA, I 21227.

Paratypes: W.A.: 2 ♂♂; 1 ♀, WAMA, SAMA.

Colour: Head, antennae, pronotum coppery-bronze. Elytra black with blue and purple reflections and following yellow markings on each elytron: basal spot; pre-medial fascia covering humeral fold, touching basal margin but not reaching suture; concave anteriorly; medial spot on margin and one near suture in some specimens; large post-medial spot near margin; pre-apical spot near suture. Hairs silver.

Shape and sculpture: Head closely punctured, thin medial impressed line from base, continued as short glabrous median keel at apex, hairy. Pronotum closely punctured; prominent basal fovea projecting anteriorly for short distance as impressed line, anterior margin projecting medially; laterally rounded and narrowed from base to apex, hairy. Elytra costate, intervals flat, each with row of punctures; laterally parallel-sided basally, rounded medially and narrowed to small marginal spines; sharp sutural spine, rounded inner margin; humeral fold poorly developed, slightly angled. Ventral surface shallowly punctured, moderately hairy, hairs long.

Size: Males, 11.2 x 4.4 mm (3). Females, 11.8 x 4.6 mm (2).

Male genitalia: (Fig. 1D). Parameres angled outwards from basal piece, slightly rounded medially, rounded abruptly to apex. Apophysis of basal piece broad, rounded apically.

Remarks: The name is derived from *occidentalis* L., western.

Key to the species of *Astraeus (sensu stricto)*

1. Head with median keel..... 2
Head without median keel..... 22
2. Hairs silver..... 3
Hairs yellow..... 21
3. Part or all of anterior ventral surface red-brown..... 4
None of anterior ventral surface red-brown..... 7
4. Gular, prosternum, meso- and metasternum, coxae 2-3, abdominal segment 1 red-brown.....
..... *A. bakeri* Barker
Less of ventral surface red-brown..... 5
5. Prosternum, coxae red-brown.....
..... *A. minus* Barker
Red brown area on either side of prosternal process..... 6
6. Shorter than 7.5 mm; humeral fold well developed, acutely angled..... *A. fraseriensis* Barker
Longer than 7.5 mm; humeral fold moderately developed, angled..... *A. obscurus* Barker
7. Most or part of leg testaceous..... 8
None of leg testaceous..... 15
8. Legs 1-2 testaceous except for outer margin of femora, leg 3 testaceous except for femur.....
..... *A. dilutipes* van de Poll
Less of leg than above testaceous..... 9
9. Tibiae, tarsomeres 1-2 testaceous.....
..... *A. smythi* Barker
Less of leg than above testaceous..... 10
10. Tibiae testaceous, distal tips blue, tarsomere 1 testaceous..... *A. jarratensis* sp. nov.
Less of leg than above testaceous..... 11
11. Distal tips of tibiae testaceous, tarsomeres 1-2 testaceous, distal tips blue, *A. williamsi* sp. nov.
Less of leg than above testaceous..... 12
12. Tips of tibiae and tarsomere 1 testaceous..... 13
Tarsomere 1 testaceous.....
..... *A. montaneensis* Barker
13. Usually shorter than 7 mm.....
..... *A. pygmaeus* van de Poll
Usually longer than 7 mm..... 14
14. Humeral fold well developed; acutely angled.....
..... *A. mastersi* MacLeay
Humeral fold well developed, angled.....
..... *A. samueli* Saunders
15. Humeral fold moderately developed, angled..... 16
Humeral fold poorly developed, slightly angled..... 17

16. Head green and coppery purple or blue-green..... 17
 Head black..... 18
17. Head, pronotum green and coppery purple.....
 Head blue-green, pronotum with medial, cordiform purple mark, anteriorly green, laterally blue,.....
 *A. intricatus* Carter
 *A. blackdownensis* Barker
18. Broad, rounded species..... *A. globosus* Barker
 Elongate species..... *A. watsoni* Barker
19. Body blue; elytra with 2 yellow fascia.....
 *A. fraterculus* van de Poll
 Body black or coppery-bronze..... 20
20. Body black; elytra with numerous yellow spots.....
 *A. crassus* van de Poll
 Body coppery-bronze; each elytron with yellow fascia and 4-5 yellow spots..... *A. occidentalis* sp. nov.
21. Elytra with 3 yellow fascia, red areas.....
 *A. major* Blackburn
 Elytra with 2 yellow fascia, no red.....
 *A. navarchis* (Thomson)
22. Body elongate and cylindrical..... 23
 Body tear-drop shaped..... 24
23. Pronotum conically elevated medially.....
 *A. prothoracicus* van de Poll
 Pronotum convex medially.....
 *A. elongatus* van de Poll
24. Sutural spine with rounded inner margin..... 25
 Sutural spine with straight inner margin..... 37
25. Legs red-brown colour..... 26
 Legs other than red-brown colour..... 27
26. Elytra marked with spots and fascia.....
 *A. macmillani* Barker
 Each elytron with 2 vittae *A. vittatus* van de Poll
27. Head, pronotum, legs metallic brown or bronze.....
 *A. flavopictus* C & G
 Head, pronotum, legs other than brown or bronze..... 28
28. Humeral fold well developed, angled..... 29
 Humeral fold moderately or poorly developed..... 30
29. Head black or coppery purple; ventral surface coppery-purple.....
 *A. adamyi* Barker
 Head blue or green; ventral surface blue-green.....
 *A. simulator* van de Poll
30. Humeral fold moderately developed, angled..... 31
 Humeral fold poorly developed, slightly angled..... 32
31. Pronotum laterally rounded from base to apex.....
 *A. crockerae* Barker
 Pronotum parallel-sided at base, rounded, indented to apex.....
 *A. badeni* van de Poll
32. Basal spot touching basal margin of elytron.....
 *A. carnabyi* Barker
 Basal spot not touching basal margin of elytron..... 33
33. Elytron with 2 spots and 2 fascia or 4 spots and a fascia..... 34
 Elytron with 6 spots and a fascia, 7 spots or 8 spots..... 35
34. Head pronotum and elytra black.....
 *A. meyrickti* Blackburn
 Head pronotum and elytra black, with blue and purple reflections..... *A. aridus* sp. nov.
35. Each elytron with 6 spots and a fascia or 8 spots.....
 *A. jansoni* van de Poll
 Each elytron with 7 spots..... 36
36. Pronotum parallel-sided from base to middle, strongly rounded and narrowed to apex; dorsally convex in lateral profile.....
 *A. oberti* van de Poll
 Pronotum gradually rounded laterally, narrowed from base to apex; dorsally flattened in lateral profile.....
 *A. carteri* Barker
37. Head with frontal spot..... *A. princeps* sp. nov.
 Head without frontal spot..... 38
38. Head with shallow median sulcus.....
 *A. guerlingi* Barker
 Head with deep median sulcus..... 39
39. Head with basal median sulcus; pronotum laterally inflated, medial oval patch of hexagonal cells.....
 *A. cyaneus* Kerremans
 Head with apical median sulcus; pronotum laterally rounded, no medial hexagonal cells.....
 *A. caledonicus* Fauvel

New locality records

A single female specimen of *A. irregularis* van de Poll was collected by Mr E. E. Adams and myself at Blackdown Tableland, Qld, on 17.I.1979 on the foliage of *Casuarina inophloia*. This is a common W.A. species recorded from S. Aust. by Barker (1977). In the revision of *Astraeus* (Barker 1977) I did not record *A. jansoni* van de Poll outside of S. Aust. except for a doubtful Queensland record. Carter (1929) listed the species as occurring in the Blue Mts. I have examined Carter specimens in the SAMA collection from the Blue Mts and more recent material collected by Mr S. Watkins on

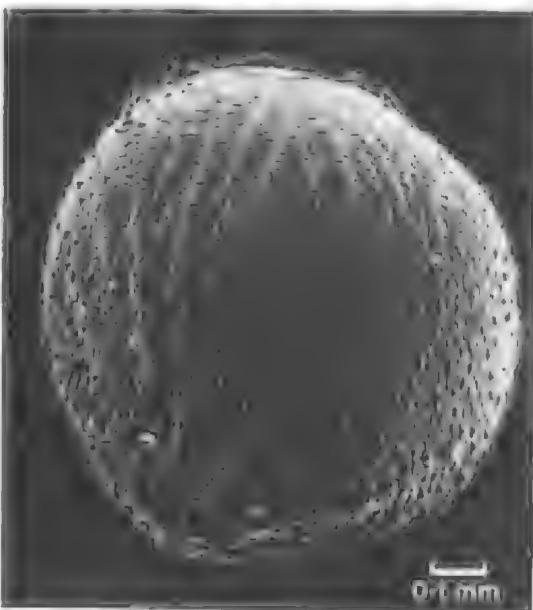


Fig. 3. S.E.M. micrograph of the elytron of *Astraeus pygmaeus* van de Poll

Callitris muelleri at Wentworth Falls and Kings Tableland in the Blue Mts and confirm them to be *A. jansoni*.

Egg of *A. pygmaeus van de Poll*

A female specimen of *Astraeus pygmaeus* captured by me 24 km east of Armidale, N.S.W., on 19.xii.1989, laid 13 eggs onto the cardboard label in the vial in which it was placed. These hatched approximately 28 days later. The hard sculptured chorion of an egg from which a larvae hatched is illustrated (Fig. 3). Crowson (1981) indicated that most beetles have smooth eggs with a soft surface. A micropyle cannot be distinguished, but a row of tubercles, each pierced by an aeropyle, is clearly visible around the margin (Fig. 4). The eggs are oval with a flat ventral surface. The larvae emerged through the ventral surface and burrowed directly into the label. The chorions adhered to the label and covered each individual gallery. Presumably the same happens in the field situation. These are the first eggs of Australian buprestids that I have seen.

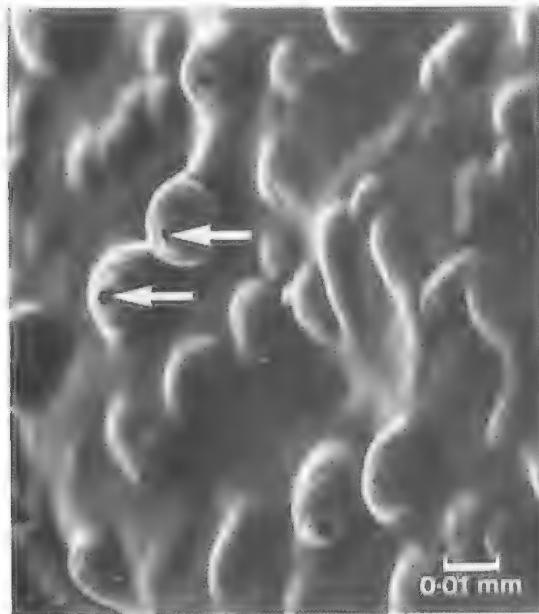


Fig. 4. S.E.M. micrograph of aeropyles (arrowed) on chorion of *Astraeus pygmaeus*.

Stigmodera (Castiarina) garnettensis sp. nov. FIGS 1G,5

Holotype: ♂, Mt Garnett, Qld, 24.ii.1989, G. Wood, I 21228 SAMA.

Allotype: ♀, Mt Garnett, Qld, 24.ii.1989, J. Hasenpusch, I 21229 SAMA.

Paratypes: Qld: 1 ♀, Mt Molloy, 9.ii.1987, G. Wood, GWQA; 2 ♀♀, Kuranda, 6/8.i.1989, J. Hasenpusch, JHQA; 1 ♀, Mt Garnett, 20.ii.1989, G. Wood, GWQA; 1 ♂, Mt Garnett, 21.ii.1989, J. Hasenpusch, JHQA; 2 ♂♂, 3 ♀♀, 22.ii.1989, J. Hasenpusch, JHQA; 5 ♂♂, 2 ♀♀, same data as allotype, JHQA; 5 ♂♂, 6 ♀♀, Mt Garnett, 21/22.ii.1989, G. Wood, GWQA; 10 ♂♂, same data as holotype, GWQA; 1 ♀, Mt Garnett, 26.ii.1989, G. Wood, GWQA.

Colour: Male (Fig. 5A). Head, antennae and pronotum coppery-purple. Scutellum green with coppery-purple reflections. Elytra yellow with following markings either black with coppery-purple reflections, or dark blue with green reflections: variable basal mark, continuous with basal margin, not reaching lateral margins, reduced to basal margin and extension along suture in one specimen; post-medial fascia reaching margin; apical mark. Ventral surface coppery purple. Legs green with coppery-purple reflections. Hairs silver. Female (Fig. 5B). Head, antennae and pronotum green with yellow reflections, occasionally head and pronotum coppery-bronze. Scutellum green. Elytra yellow with following dark blue markings: broad basal fascia; broad post-medial fascia; basal mark. Ventral surface green with yellow reflections. Legs blue-green. Hairs silver.

Shape and Sculpture: Head closely punctured, median sulcus, short muzzle. Antennae, segments: 1–3 obconic; 4–11 toothed. Pronotum closely punctured, narrow basal fovea extending forwards to middle as glabrous line, basal notches on each side more marginal than medial; apical margin projecting medially, basal margin barely bisinuate; laterally angled outwards from base, rounded one third of distance from base, bulbous, tapered to apex. Scutellum scutiform, punctured, flat. Elytra punctate-striate, intervals convex, punctured; laterally angled out from base, rounded at humeral callus, concave, rounded posteromedially, abruptly rounded to spineless apex; apices diverging, apical margin subserrate. Ventral surface with shallow punctures, edges of abdominal segments glabrous, moderately hairy, hairs medium length. S, rounded in both sexes.

Size: Males, $14.2 \pm 0.15 \times 5.8 \pm 0.07$ mm (24). Females, $15.4 \pm 0.27 \times 6.6 \pm 0.12$ mm (17).

Male genitalia: (Fig. 1G). Short and broad. Parameres angled outwards from basal piece, rounded posteromedially then parallel-sided, rounded to apex. Apophysis of basal piece medium

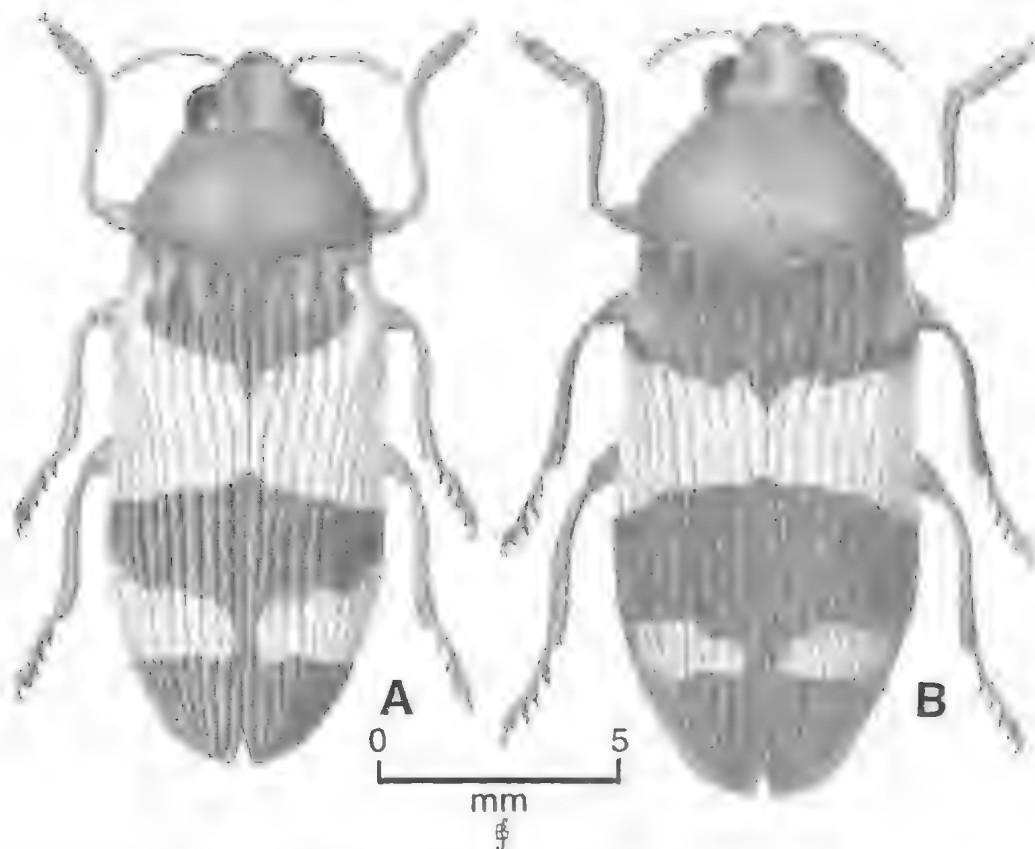


Fig. 5. Habitus illustrations of the following species: A. *Stigmodera garnettensis* sp. nov. male, B. *S. garnettensis* sp. nov. female.

width, tapered to rounded apex. Medium lobe pointed, sides obtusely angled away.

Remarks: This is a member of the *S. cruenta* Saunders species group as well as *S. flava* Saunders, *S. ovata* Barker, *S. pallas* Blackburn and *S. vallisi* Dequert. Like *S. vallisi* the sexes are dimorphic and can be separated on colour and pattern differences. In the male genitalia of *S. vallisi* (Fig. 1H) the apophysis of the basal piece is narrower. The specific name is derived from the type locality.

***Stigmodera (Castiarina) wellsae* sp. nov.**
FIGS 1I, 2H

Holotype: ♂, Portland, Vic., 21.xi.1944, E. Smith, NMVA.

Allotype: ♀, 20 km N Moe, Vic., 8.xi.1979, A. Wells, SAMA 121230.

Paratypes: Vic.: 1 ♂, 1 ♀, Emerald, 3.xii.1907, Jarvis, NMVA, SAMA; 3 ♂♂, Grampians, Nov.

1950, B. Given, NMVA; 4 ♂♂, Portland, 6.xii.1918, NMVA; 1 ♂, Ferntree Gully, 30.x.1919, NMVA; 1 ♂, Portland, NMVA; 1 ♂, 1 ♀, 'Taruna', Croydon, S. W. Fulton, NMVA; 1 ♀, Belgrave, 19.xi.1946, F. E. Wilson, NMVA; 1 ♀, Healsville, Nov. 1916, NMVA; 1 ♀, Monbulk, 12.xi.1902, Jarvis, NMVA; 1 ♀, Boulora, 4.xii.1954, A. L. Brown, NMVA; 1 ♀, locality indecipherable, 14.xi.1903, NMVA; 1 ♂, 4 ♀♀, no data, NMVA; 4 ♂♂, 5 ♀♀, Mt Rosea, Grampians, 15.xi.1950, G. F. Gross, SAMA; 1 ♂, Hall's Gap, Grampians, 14.xi.1950, LeSouef, SAMA.

Colour: Head and antennae blue with bronze reflections. Pronotum blue with bronze reflections medially, yellow laterally. Scutellum blue with bronze reflections. Elytra yellow with following blue markings with blue-green reflections: very broad basal mark only touching margin at humeral callus; broad post-medial fascia; pre-apical spade-shaped mark, reduced in holotype and allotype to short horizontal bar, all marks connected along suture to apex. Hairs silver.

Shape and Sculpture: Head closely punctured, median sulcus, short muzzle. Antennae, segments: 1–3 obconic; 4–11 toothed. Pronotum closely punctured, narrow basal fovea extending anteriorly to apical margin as impressed line, shallow fovea at each basal angle; apical margin projecting medially, basal margin barely bisinuate; laterally rounded from base to apex, widest medially. Scutellum scutiform, few punctures, flat. Elytra punctate-striate, intervals convex, punctured; laterally angled out from base, rounded at humeral callus, concave, rounded posteromedially and narrowed to spineless apex; apices hardly diverging, apical margin rough. Ventral surface with shallow punctures, edges of abdominal segments glabrous, moderately hairy, hairs short. S₇: male truncate; female rounded.

Size: Males, 10.1 ± 0.18 x 4.0 ± 0.09 mm (19). Females, 10.5 ± 0.19 x 4.1 ± 0.10 mm (16).

Male genitalia: (Fig. 11) Short. Parameres parallel-sided basally, rounded posteromedially, parallel-sided, rounded apically. Median lobe sharp, sides

acutely angled away. Apophysis of basal piece medium-width, tapered, flattened apically.

Remarks: Member of the *S. distinguenda* Saunders species group together with *S. arida* Barker, *S. blackdownensis* Barker, *S. garrawillae* Carter, *S. grata* Saunders, *S. militaris* Carter, *S. subgrata* Blackburn, *S. supergrata* Barker, *S. watkinsi* Barker. It is closest to *S. watkinsi* but differs in having blue markings on the dorsal surface whereas those in *S. watkinsi* are green, a different distribution; different male genitalia (Barker 1988; Fig. 1E). Specimens in the NMVA had been misidentified as *S. grata* Saunders. Named after Dr Alice Wells.

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TRILOBITES AND THEIR TRAILS IN A BLACK SHALE: EARLY CAMBRIAN OF THE FLEURIEU PENINSULA, SOUTH AUSTRALIA

BY RICHARD J. F. JENKINS & PAM HASENOHR*

Summary

An Early Cambrian trilobite from the Normanville Group in the Sellicks Hill area, Fleurieu Peninsula, South Australia is here identified as *Ivshiniellus briandailyi* sp. nov. The trilobites occur in 'black shale' in close stratigraphic proximity to a bedding-plane surface showing trails made by large trilobites. The environment was below storm-wave base and the traces indicate that the black shale deposited in water sufficiently well oxygenated to support large metazoans with a presumed oxidative metabolism. Black coloration in shales may not be taken as a necessary indication of anoxic bottom waters.

KEY WORDS: new species, conocoryphid trilobite, trace fossils, black shale, Cambrian, South Australia.

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JENKINS, R. J. F. & HASENOHR, P. (1989) Trilobites and their trails in a black shale: Early Cambrian of the Fleurieu Peninsula, South Australia. *Trans. R. Soc. S. Aust.* 113(4), 195–203, 30 November, 1989

An Early Cambrian trilobite from the Normanville Group in the Sellicks Hill area, Fleurieu Peninsula, South Australia is here identified as *Iyshimelitus brundalysi* sp. nov. The trilobites occur in 'black shale' in close stratigraphic proximity to a bedding-plane surface showing trails made by large trilobites. The environment was below storm-wave base and the traces indicate that the black shale deposited in water sufficiently well oxygenated to support large metazoans with a presumed oxidative metabolism. Black coloration in shales may not be taken as a necessary indication of anoxic bottom waters.

KEY WORDS new species, conocoryphid trilobite, trace fossils, black shale, Cambrian, South Australia.

Introduction

Jago *et al.* (1984) reported the first discovery of trilobite remains in the Early Cambrian Normanville Group on Fleurieu Peninsula, South Australia. They described two specimens of a conocoryphid trilobite from the Heatherdale Shale in the Sellicks Hill area (Fig. 1), but considered the material so poorly preserved as to preclude formal description. While exploring the same site during late 1984, one

of us (P.H.) discovered a spectacular trace fossil made by an arthropod. Further searching revealed two more body fossil remains of trilobites. This paper reports these new discoveries.

Of the new trilobite remains, one shows the cephalon and anterior thorax and the other is a fragmentary thorax. They were discovered on surfaces that had split open to the weather, and the very incomplete specimen is preserved essentially as a ferruginised film. The more complete individual, an external mould, resembles specimen SAM P24321 described by Jago *et al.* (1984) and provides

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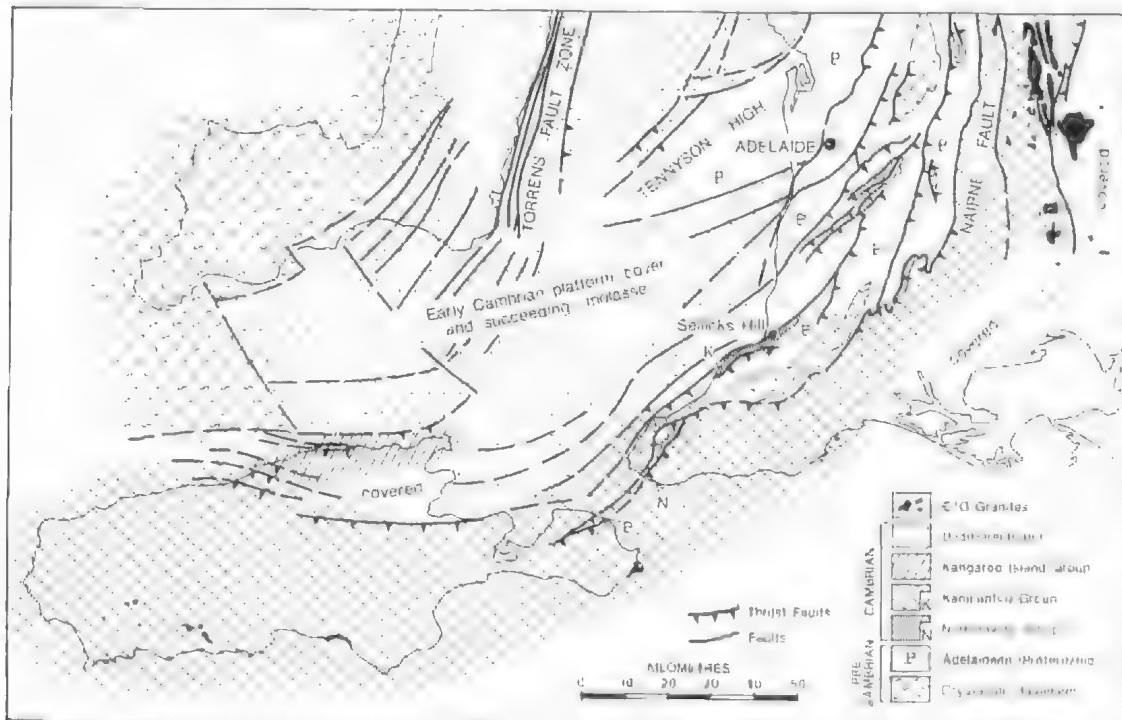


Fig. 1. Locality map showing find of trilobites and trace fossils at Sellicks Hill, and the placement of this discovery in relation to the framework of the Adelaide Fold Belt and adjacent foreland basin.

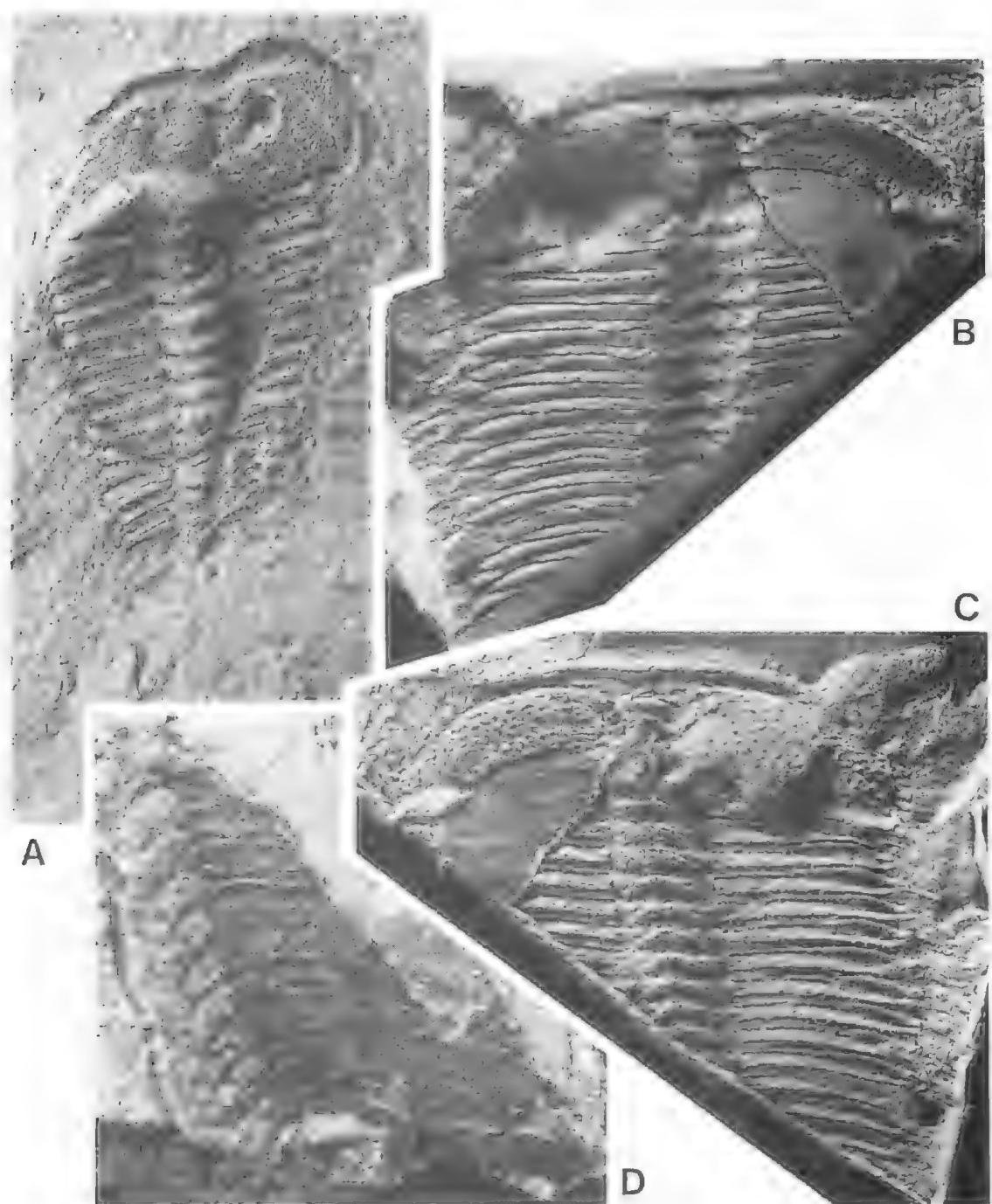


Fig. 2A-C. *Ivishmellus briandulyi* nov. sp.: A, holotype SAM P24321, with anterior glabella relatively well preserved and composite mould of hypostome present, x3; B, C, paratype SAM P24844, B, external mould and C, silicon rubber cast of individual made from mould, both x1.5. D. concomorphid gen. et sp. indet, SAM P24845, fragment photographed under a film of water, x1.5.

sufficient additional morphological information to justify formal description of the taxon.

The arthropod traces in near association with the body fossil specimens of the trilobites are of especial interest as the host rock represents a 'black shale' facies. Thus the traces provide an unusual palaeobiological perspective on this interesting find.

The studied specimens are registered in the Palaeontology Collection of the South Australian Museum, Adelaide (SAM).

SYSTEMATICS

Superfamily CONOCORYPHACEA Angelin, 1854

Family CONOCORYPHIDAE Angelin, 1854

Remarks: Divisions amongst the various genera of conocoryphids tend to be ill-defined due to description of cranidia alone or because many remains of these thin-shelled trilobites are markedly distorted. Furthermore, workers have tended to stress that the group is polyphyletic (Westergard 1950; Sdzu 1961; Hutchinson 1962; Rasetti 1967). On the basis of the evident positioning of the facial suture on the brim, the present form is a 'true' conocoryphid (Figs 2 & 4).

The family Conocoryphidae is rare in the Early Cambrian and much more common globally in the Middle Cambrian (Korobov 1973). Lochman-Balk & Wilson (1958) considered that the blind Conocoryphidae and Endiscidae were characteristic of extracratonic, eurytopic biofacies in the Cambrian of eastern North America and suggested that the blind condition was favoured by some important ecological factor.

Genus *Ivshiniellus* Korobov, 1966

Remarks: The better preserved of the original specimens (SAM P24321) is described as having a rearwardly directed furrow on the side of the anterior part of the glabella (Jago *et al.* 1984); medially this part of the glabella seems to have been entire and undivided. Though the front of the glabella of the new specimen is crushed, there appear to be four pairs of glabellar furrows (Fig. 3); the glabella tapers anteriorly and is somewhat constricted at about a third its length. These characteristics and other aspects of the cranidium conform to the diagnosis of the Early Cambrian genus *Ivshiniellus* Korobov, 1966. Most Cambrian conocoryphid genera show three pairs of glabellar furrows (in advance of the occipital groove). The distance the glabella reaches forwards towards the frontal border, the possible presence of a raised pre-glabella lobe, and the width of the frontal field, if it is developed, are some of the significant character-

istics important for distinguishing conocoryphids.

While Korobov (1966) compared his new genus with the Middle Cambrian taxon *Bailiella* Mathew, 1885, it is similar to the Early Cambrian *Pseudotops* Lake, 1940. Species of *Pseudotops* may show four pairs of glabella furrows, but the glabella is only weakly tapered forwards and differs from that in *Ivshiniellus* in encroaching on the frontal border.

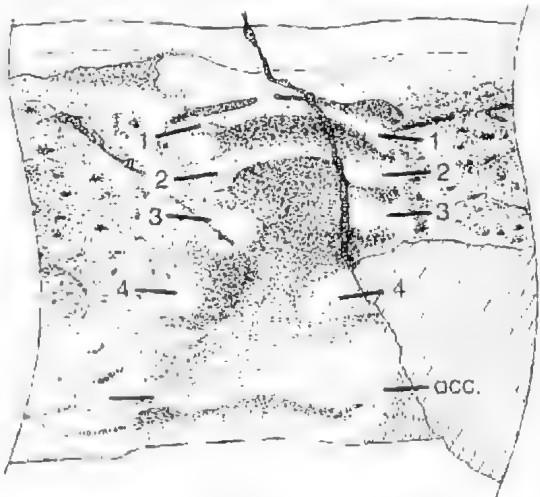


Fig. 3. Representation of the glabella and cepstral part of the cranidium of SAM P24844 showing position of the four pairs of glabellar furrows, 1–4, in advance of the occipital furrow, occ. The more anterior glabellar lobes are strongly compressed in an anteroposterior direction. Compare with Figure 2B.

Ivshiniellus briandailyi sp. nov.

FIGS 2–4

Conocoryphid sp. indet. Jago *et al.* 1984, pp. 208–210, figs. 2a–c.

Etymology: Honouring the late Dr Brian Daily (1931–1986) for his contribution to Australian geology and teaching.

Diagnosis: Brim weakly inflexed medially, cranidium encircled by border furrow and rather evenly covered by fine to coarse, pointed granules (spinules) in immature specimens, glabella almost smooth in more mature examples; pleura with acicular, weakly deflexed terminal spines; eleventh segment macropleurous.

Material: Holotype SAM P24321, lacking rearmost parts (Jago *et al.* 1984, fig. 2a, b); two paratypes, SAM P24322, rear thoracic segments and fragmentary pygidium (Jago *et al.* 1984 fig. 2c); SAM P24844, cranidium and parts of 14 thoracic segments.

Description: It is unnecessary to repeat the descriptions of the holotype and second fragment

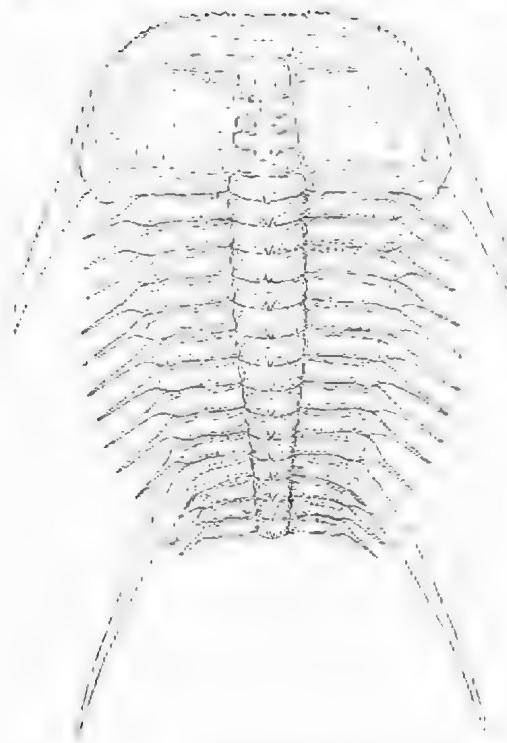


Fig. 4. Reconstruction of cephalon and major part of thorax of *Ivshiniellus briandaiyi*, sp. nov., about 2.5 times dimensions of holotype.

provided in Jago *et al.* (1984, pp. 209–210). The new specimen confirms the arcuate shape of the cephalon before, and slight median inflection of the border, as well as indicating that the facial suture is confined to the brim. In the holotype, the granulose brim is poorly preserved and is wider than might seem obvious in the previously published figures; its posterior is well-defined and the wide border furrow more finely and sparsely granulose than the central parts of the cranidium. The new remains show a nearly smooth, narrow glabella tapering forwards, with four pairs of glabella furrows directed rearwards. The fragmentary base of an occipital spine is present in the holotype.

The additional individual indicates at least 14 thoracic segments and confirms that the eleventh is macropleurous. The thin pleural ridges on the holotype show a line of 10–11 spinules or pointed granules on the anterior segments and 8–9 such granules on the posterior ones; other fine granules occur between.

Measurements: The holotype, SAM P24341, indicates an animal exceeding 25 mm in length. The distorted cranidium of SAM P24844 is 50 mm wide and the maximum width of the glabella is 8.5 mm; fourth thoracic segment about 745 mm wide,

excluding the spines and with the axis about 20.21 the width of the segment; animal in excess of 55 mm long.

Comparison: The genus includes two previously described forms, *Ivshiniellus nikolii* and *Ivshiniellus patulus* Korobov, 1966, both from the Aldanian Stage in Tuva, southeastern Siberia, within the Ezim Suite on the Ezim River. Both are represented by distorted cranidia and so any comparison with the present distorted remains must necessarily lack precision. *I. briandaiyi* resembles *I. nikolii* in the shape of the cephalon, save for the distinctive medial inflection of the frontal border; the glabella also seems narrower. *I. patulus* differs from both of the former in its pointed glabella and the somewhat quadrate shape of the fixed cheeks.

Mr J. G. Gehling has kindly provided photographs of cranidia and loaned several nearly complete dorsal exoskeletons of conocoryphid trilobites collected from the Parara Limestone at Bunyeroo Gorge in the Flinders Ranges. This material is of a taxon different to *I. briandaiyi* as the eighteenth thoracic segment is macropleurous not the eleventh, and the medial thoracic segments have remarkably long and strong pleural spines. The rather long glabella, which reaches a depressed border furrow behind the medially widened border, has three pairs of incised, backwardly directed furrows and a weak pair of depressions on the extreme anterior portion; laterally, the facial sutures cut off the major part of the brim. In its cephalic characteristics this form from the Parara Limestone shows similarities to the Early Cambrian genus *Atops* Emmons, 1844.

Conocoryphid gen. et sp. indet.

Remarks: The additional fragmentary thorax (SAM P24845) does not show the eleventh segment (counted from the most anterior segment preserved) macropleurous, and the pleural spines are more deflexed and evidently shorter than in the preceding form. However, the pleura show the characteristic wide-flat pleural grooves and narrow pleural ridges of conocoryphids. The thoracic segments are about 11.3 times as wide as long, excluding the spines, with the axis about 0.24 the width of the segment. The poor preservation has largely obliterated any surface detail.

Disarticulated thoracic segments associated with cranidia of *Ctenocephalus* Hawle & Corda, 1947, in material from the Middle Cambrian of France, show the pleural terminations narrowed abruptly and thence produced into a somewhat deflexed, slender spine. The shape of the pleural terminations in SAM P24845 is markedly similar. This specimen could be a dimorphic individual of *I. briandaiyi*.

or even represent a separate conocoryphid taxon, but basically is too fragmentary for determination.

Age of trilobite finds

The occurrence of *Ivshiniellus* on the Fleurieu Peninsula is of potential significance with respect to the timing of a major stratotectonic development within the Adelaide Fold Belt. Cambrian rocks of the Normanville Group below the Heatherdale Shale are of both basinal and shelf aspect (Daily 1963, 1976; Jago *et al.* 1986). The trilobites occur in the upper member of the Heatherdale Shale high in the section of the formation exposed (Jago *et al.* 1984). At Carrickalinga and more southerly parts of the Fleurieu Peninsula the Heatherdale Shale is abruptly succeeded by up to ca. 1300 m of turbidites of the Carrickalinga Head Formation (*sensu lato* of Daily & Milnes 1971, 1972; Milnes 1986), the basal interval of the thick psammitic and/or pelitic sediments of the Kankmantoo Complex. Sandstones of subtidal or tidal origin (Backstairs Passage Formation) succeeding the Carrickalinga Head Formation record a phase of basin filling. Jenkins (1989) identifies this overall basinal deepening and shallowing as the 'Rauhndjeri/Jadliaura stratotectonic cycle' and the organic-rich sediments (Foster *et al.* 1985) of the Heatherdale Shale may be considered as the 'euxulic' phase marking the start of rapid subsidence associated with renewed lithospheric extension.

The likely age of *Ivshiniellus* in Siberia is late Aldanian (Korobov 1973; Jago *et al.* 1984) or medial Early Cambrian, and the comparable genus *Pseudatopw* also occurs in the ?mid Early Cambrian of eastern North America and the British Isles. The present finding that *I. briandailyi* and a conocoryphid from Bunyeroo Gorge are different taxa weakens the claim of Jago *et al.* (1986) that conocoryphids suggest a correlation between the Heatherdale Shale and higher parts of the Parara Limestone in the Flinders Ranges, though on a tectonic basis the onset of deposition of the dark, nodular offshore facies of the latter formation may well have corresponded with the deepening signalled by the Heatherdale Shale (see Jenkins 1989).

Trace Fossils

An upper-surface bedding plane at the trilobite site shows a relatively well preserved arthropod trail extending over a distance of 80 cm, parts of two other trails probably made by large trilobites and a poorly preserved section of the back-filled burrow produced by a worm-like creature (Figs 5-6). This surface has been preserved due to an unusual circumstance

The arthropods evidently moved over a relatively fine-grained and soft, muddy substrate with the ends of their limbs making deep impressions. Had this surface been subsequently buried by further silt, the cleavage now present in the rock due to deformation (Cambro-Ordovician Delamerian Orogeny) would probably preclude splitting along the particular bedding surface. However, the traces were buried by a 3.5 cm thick bed now comprising intergrown phyllosilicates and minor fine (<0.1 mm diameter), angular quartz grains, which are commonly amalgamate and show undulose extinction. The quartz is probably detrital. XRD analyses of the rock confirm visual observation that the bed is inhomogeneous with a (less weathered?) fraction comprising predominantly illite 2M₁, minor muscovite M₁, and kaolinite-smectite, and a second (weathered?) fraction including illite and Ca montmorillonite. Iron rich opaques are concentrated in parts. Illite 2M is consistent with a paragenesis involving deep burial and alteration of possible older mineral phases. The bed is continuous along strike over an exposure distance of 60 m and thickens slightly towards the south (up to 4.5 cm). In places, obvious granular components that are apparently 'reliefs' of the original sedimentary particles grade in size from ~0.5–1.2 mm near the base of the bed to ~0.1 mm at the top.

The granular aggregates of phyllosilicates possibly represent the highly altered components of an air-fall tuff that mixed with a small amount of detrital material and formed a slurry which buried and moulded the trilobite traces. During modern weathering a line of parting developed subjacent to the underlying siltstone such that a very thin veneer of granular material still adheres to and completely covers the traces.

The trail traced over 80 cm consists of sub-parallel rows of rather closely spaced imprints of ambulatory limbs and averages 75 to 80 mm in width. The individual imprints tend to be set obliquely or en-echelon and the best preserved are about 10 mm long. This trace is of the form illustrated by Bellacher (1955, fig. 1a, b) and was evidently made by a perambulating trilobite with its body axis aligned in the direction of travel. In one area it is overlapped by a crudely segmented trace made by a worm-like animal. Nearby exposures in the Heatherdale Shale show much better preserved examples of what is probably this same trace occurring in association with numerous burrows of a relatively large form of *Planolites* Nicholson, 1873. The segmented trace is probably of endogenic origin and well preserved examples show a regular back-filling of large ovate faecal pellets arranged transversely.

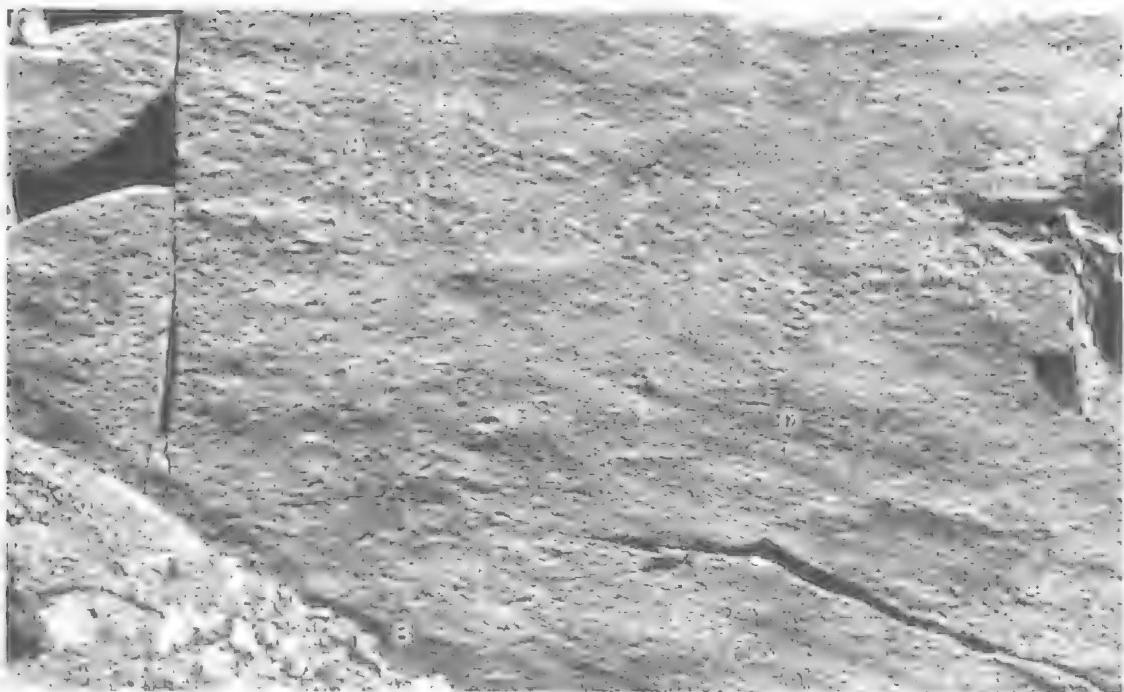


Fig. 5. Bedding plane below tuff horizon, showing trace fossils made by trilobites, A-C, and structure, D, attributed to an unknown worm-like animal. A-A', trace made by perambulating trilobite with body aligned in direction of travel; B-B', marks made by large trilobite moving obliquely; C-C', indication of a trilobite travelling relatively quickly. Scale bar equivalent to 20 cm.

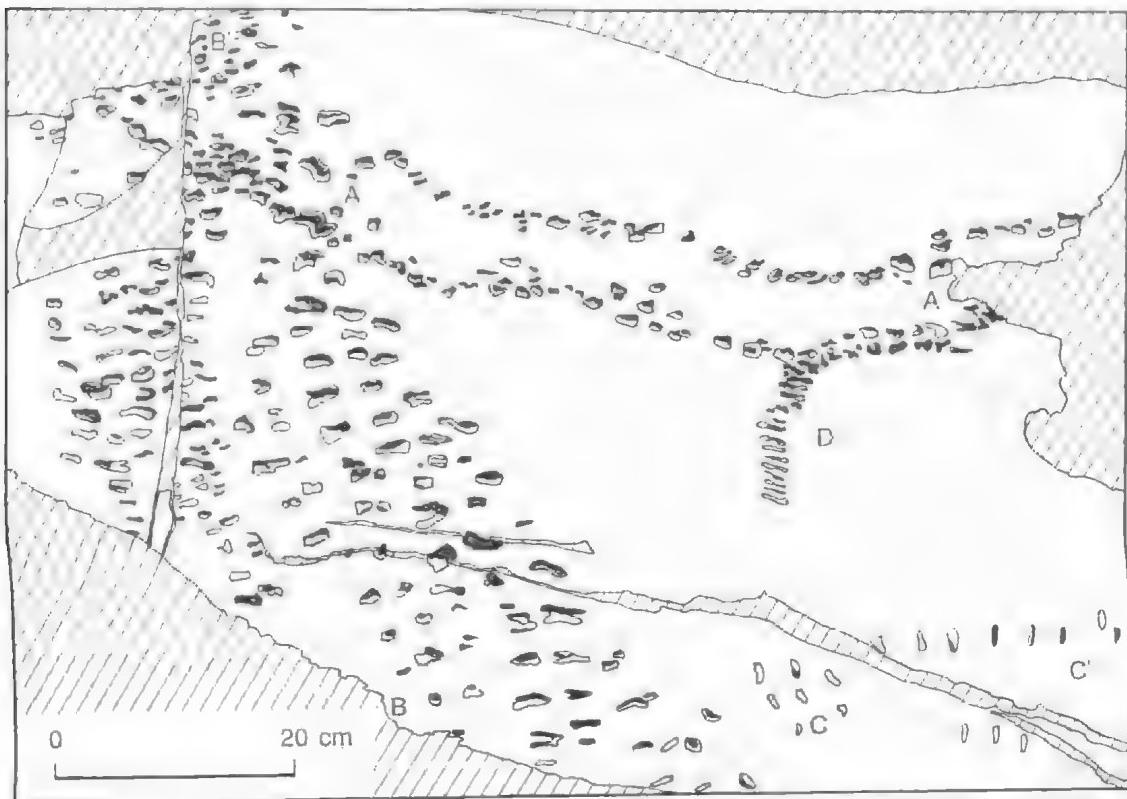


Fig. 6. Representation of bedding surface portrayed in Fig. 5 indicating the several sets of markings made by trilobites (A-A', B-B', C-C') and another unknown animal (D).

The two other traces show relatively widely spaced series of imprints interpreted as the impressions of the tips of the telopodites of trilobites. In the larger trace, the individual imprints are up to 20 mm long and on one side of the complete trail are arranged in rather irregular rows positioned in an en-echelon manner. This sort of marking is well explained by Seilacher (1955, fig. 1e, f) and indicates a trilobite moving obliquely crab-wise, perhaps partly in response to a gentle side current. The tips of the limbs which formed the marks on either side of the trace spanned approximately 23 cm, indicating a quite large animal. The imprints of the remaining trace are widely spaced and suggest a smaller animal travelling relatively quickly with the body aligned in the direction of travel. These marks are not especially distinctive (and were only seen in certain lighting) but are comparable with some of the large trilobite trails occurring in the late Early to Middle Cambrian Kangaroo Island Group of Daily (1956), on the north coast of Kangaroo Island.

The body fossil remains of the trilobites described herein occurred respectively 1.6 m stratigraphically below the surface with trilobite trails (SAM P24844) and 88 cm above this surface (SAM P24845). The traces suggest that trilobites were live inhabitants of the bottom environment.

Palaeobiological significance

The thinly laminated argillites of the upper member (~240 mm thick) of the Heatherdale Shale are almost entirely flat bedded and certainly accumulated at depths below storm wave base (cf. Jago *et al.* 1986). A single rippled surface observed may reflect localised bottom currents. Considering the thickness of the succeeding turbidites, the depth of water in the depositional environment was probably of the order of hundreds of metres.

Jago *et al.* (1984) cite and illustrate apparent mudcracks in the Heatherdale Shale (their fig. 4) as possibly indicating a shallow environment of deposition but they concede that the cracks may have formed due to synaeresis. Dzikowski & Walton (1965) illustrate (their figs 112 & 113) comparable cracks in turbidites.

Trilobite trails occur abundantly in parts of the late Early to Middle Cambrian sequence on the north coast of Kangaroo Island (Sprigg 1955; Daily *et al.* 1979). Examples of such trails up to 10–12 cm in width are especially numerous in intervals of these rocks deposited in tidal and subtidal facies. This association of trilobite trails in shallow-water sediments is common world wide during the older Palaeozoic and constitutes the *Cruiziana* facies of Seilacher (1961). Thus it is apparent that trilobites

had an ordinary oxidative kind of metabolism such as is characteristic of modern, free living arthropods and metazoans in general.

The arthropod trails in the Heatherdale Shale suggest relatively large animals moving over the bottom in some numbers. The implication is that the body fossil remains of trilobites were part of an indigenous population and not isolated individuals somehow transported into the environment by chance. Presuming an oxidative metabolism for the trilobites, and the worm-like creatures responsible for various burrowed horizons, the bottom waters of the Heatherdale Shale environment were clearly not uniformly anoxic and must have been at least moderately well oxygenated at the times of bioturbation. This contradicts the commonly held opinion that black shales characterize oxygen starved basins; fluctuating oxygen tensions may be more likely (Morris 1980; Kaufman 1982; Küspert 1982; Wetzel 1982; Conway Morris 1985).

By measuring the displacement of a conveniently sized plaster model of a trilobite, the soft tissue mass of the animal which made the 23 cm wide trail may be estimated at ~500 g. With reference to fig. 8.6 of Alexander (1979), the oxygen consumption of an animal of this size may have been about $0.045 \text{ ml gm}^{-1} \text{ hr}^{-1}$ or for the whole organism, 23 ml hr⁻¹. Runnegar (1982) demonstrated that the surface area of the respiratory organs (e.g. gills) of aqueous animals is approximately proportional to the body mass; this suggests a respiratory exchange surface of ~500 cm² for the trilobite. Application of equation 13.5 of Alexander (1979, p. 279) indicates that the partial pressure between the sea water and blood over the respiratory surface needed to supply the required oxygen consumption is ~0.06 atm. Assuming that the respiratory pigment in the animal's blood was saturated at 0.02 atm, the minimum oxygen concentration in the sea water necessary for the trilobite was ~0.08 atm or ~38% PAI (~60 mm Hg of O₂). This value lies within the medial part of the spectrum of oxygen concentrations in the oxygen minimum layer of modern oceans, effectively 2.5% PAI to 60% PAI (Barnes & Hughes 1982, fig. 1.9).

There is currently a renewed wave of speculation concerning the possible increase of atmospheric oxygen during the late Precambrian and its relationship to the emergence of the metazoa and higher plant life (Rennegar 1982a, b and pers. comm.; Glaessner 1983, 1984). The present example suggests that simple observation of dark coloration in parts of Precambrian sequences (e.g. grey and black phyllites in the 'Torreysian' Series of the Adelaidean) is unlikely to give reliable information on ambient oxygen tensions. The coloration of

shales will also reflect diagenetic processes and the effects of incipient metamorphism; for example recrystallization of hematite to specularite may cause beds to become almost black (Clemmey & Badham 1982).

I. brundalli is remarkable for the long genal spines, the attenuated spines on the pleurites and its macropleurous eleventh segment. Similar long spines in odontopleurid trilobites have been considered to have functioned in helping to support the animals on the sea bottom, either during 'resting' or while they were feeding with the aid of currents passing between the substrate and the lower side of the thorax (Wittington 1956a, b; Clarkson 1969; for a different opinion see Bergström 1973). Such an adaptation is consistent with *I. brundalli* inhabiting a soft muddy bottom. Because of the

lack of streamlining brought about by the spines the trilobite was probably not an agile swimmer, and this accords with the finding of trackways in close proximity to its remains. However, the trackways indicate larger animals than the body fossil specimens and there is no way of telling whether the traces were made by more mature individuals of conocoryphids or other trilobites known to reach large size locally, such as *Redlichia* Cossmann 1902 (see Conway Morris & Jenkins 1985). A host of modern day creatures have adapted to inhabit caves and other dark places and become secondarily blind, and loss of sight in conocoryphids would have posed no disadvantage if these primal denizens of the deep were bottom dwellers who lived below the effective penetration of light, sustained primarily on settled detritus.

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**REDISCOVERY OF *PRIMOVULA* (*P.*) *HELENEAE* CATE AND
DESCRIPTION OF A NEW SPECIES OF *CRENAVOLVA* FROM SOUTH
AUSTRALIA (MOLLUSCA: GASTROPODA: OVULIDAE)**

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Summary

The first live collected specimens of the South Australian allied cowrie *Primovula* (*P.*) *heleneae* Cate, 1973 are recorded. This species, previously known from a single shell collected prior to 1908, is redescribed, and details of the animal and its habitat given. *Crenavolva cruenta* sp. nov., is described from Spencer Gulf, S.A.; it most closely resembles *C. striatula* and *C. verconis* but is distinguished by its more elongate form, more produced ends and colour pattern.

KEY WORDS: Gastropoda, Ovulidae, South Australia, *Primovula heleneae*, *Crenavolva*, new species, habitat.

REDISCOVERY OF *PRIMOVULA (P.) HELENEAE* CATE AND DESCRIPTION OF A NEW SPECIES OF *CRENAVOLVA* FROM SOUTH AUSTRALIA (MOLLUSCA: GASTROPODA: OVULIDAE)

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Summary

GOWLETT-HOLMES, K. I. & HOLMES, N. J. C. (1989) Rediscovery of *Primovula (P.) heleneae* Cate and description of a new species of *Crenavolva* from South Australia (Mollusca: Gastropoda: Ovulidae). *Trans. R. Soc. S. Aust.* 113(4), 205-214, 30 November, 1989.

The first five collected specimens of the South Australian allied cowrie *Primovula (P.) heleneae* Cate, 1973 are recorded. This species, previously known from a single shell collected prior to 1908, is redescribed, and details of the animal and its habitat given. *Crenavolva crenata* sp. nov., is described from Spencer Gulf, S.A.; it most closely resembles *C. striatula* and *C. verconis* but is distinguished by its more elongate form, more produced ends and colour pattern.

Key Words: Gastropoda, Ovulidae, South Australia, *Primovula heleneae*, *Crenavolva*, new species, habitat.

Introduction

Three species of the allied cowrie family Ovulidae are recorded from South Australia: *Crenavolva verconis* (Cotton & Godfrey, 1932), *Primovula (P.) heleneae* Cate, 1973, and an *Aplysia* sp. (Coleman 1981). All are regarded as very rare. The first two species are known from single specimens dredged dead prior to 1908 (Verco 1908, as *Ovula formosa*).

Off Douglas Point in northern Spencer Gulf, S. Aust., one of us (NJCH) found a number of allied cowries living on fans of the gorgonian corals *Euplexaura* sp. and *Echinogorgia* sp. in 10-15 m depth. These specimens were identified as *Primovula (P.) heleneae* Cate, 1973, (living on *Euplexaura* sp.), and an undescribed species of *Crenavolva*, (living on *Echinogorgia* sp.). Here we describe the new species of *Crenavolva*, redescribe *P. (P.) heleneae*, and include details of the animal and its habitat.

Materials and Methods

The material reported here is deposited in the South Australian Museum, Adelaide (SAM), Australian Museum, Sydney (AM), Museum of Victoria, Melbourne (NMV), Northern Territory Museum of Arts & Sciences, Darwin (NTM), Queensland Museum, Brisbane (QM), Western Australian Museum, Perth (WAM), Tasmanian Museum and Art Gallery, Hobart (TM) and National Museum of New Zealand, Wellington (NMNZ). Living material was collected by "SCUBA" and "Hookah" diving and using a Smith-McIntyre grab dredge. Underwater photographs of the living animals were taken using Nikonnos III and Nikonnos V cameras with macro extension

tubes and electronic flash units. Wet material was preserved in 75% methylated ethanol solution or 2% formalin/propylene glycol solution. Radulae were prepared for examination under scanning electron microscope (SEM) after the method of Bandel (1984). Colour descriptions follow Kornerup & Wanscher (1978).

Primovula (Primovula) heleneae Cate, 1973
FIGS 1, 3, 4.

Ovula formosa: Verco, 1908, p. 342 (non Adams & Reeve 1848).

Prosmilia verconis: Cotton & Godfrey, 1932; p. 26, pl. 1, fig. 15 (in part).

Pellasimnia verconis: Tredale, 1935, p. 105; Cotton, 1959, p. 368, (in part).

Primovula (Primovula) verconis: Schilder, 1941, p. 107, (in part).

Neosimnia (Pellasimnia) verconis: Allan, 1956, p. 130, pl. 14, fig. 40 (in part).

Primovula (Primovula) heleneae Cate, 1973a; p. 43-4, fig. 89.

Type: Holotype (SAM D15943), part of the type series examined by Cotton & Godfrey (1932); a paratype of *Prosmilia verconis*.

Type locality: Holotype dredged in Gulf St Vincent or Spencer Gulf, S. Aust., by J. C. Verco; the holotype of *P. verconis* was dredged off St Francis Island, S. Aust., by J. C. Verco.

Other material: SAM D17973 (4 + eggs, in spirit), SAM D17975 (2, dry) Douglas Point, northern Spencer Gulf, S. Aust., N. J. C. Holmes, 17.vi.1987; SAM D18434 (13, dry), SAM D18435 (8, in spirit) Douglas Point, northern Spencer Gulf, S. Aust., N. J. C. Holmes, 5.v.1988.

Species description: Small allied cowrie, adult length 9.15-13.80 mm, mean 10.77 mm ± 1.004. Elongate; both ends slightly produced, posterior end more so; widest part of dorsum in posterior 1/3 (Fig. 3E).

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Fig. 1. *Primovula (P.) heleneae*, two adults, one with partially extended mantle, on the gorgonian coral *Euplexaura* sp.



Fig. 2. *Crenavolva cruenta* sp. nov., two adults with partially extended mantles on the gorgonian coral *Echinogorgia* sp.

Dorsum (Fig. 3A) sculptured with numerous transverse wavy striae; funiculum prominent, with three weak transverse ridges. Base (Fig. 3B) concave, outer lip and parietal-columellar lip flat and inward sloping; aperture narrow with a strong fossula, both sides strongly calloused. Parietal-columellar base smooth but with body whorl striae visible beneath the callus. Outer lip with weak transverse ridges posteriorly, inner margin slightly dentate posteriorly; outer margin with three to ten slight to prominent nodules at posterior end, more prominent in smaller shells; usually with one to three slight nodules at anterior end.

Posterior canal somewhat produced, with a basally projecting terminal knob dividing canal into distinct left and right channels (Figs 3C, 3D). Anterior canal shallow "U"-shaped, slightly flaring and turned to the right, bordered on both sides by distinct and slightly projecting terminal ridges.

Shell pastel red to pale orange to greyish yellow, anterior and posterior tips usually orange; paler band across widest part of dorsum; columellar callus, outer lip and labial callus all paler than dorsum.

Animal mantle lobes (Fig. 1) with no papillae; translucent pastel red to dark orange, with irregular, reddish brown patches varying in size, area immediately around each patch not patterned, remainder of mantle patterned with slightly raised, white dots. Foot pinkish white; anterior dorsal foot with a series of prominent, vertical lamellae; posterior dorsal foot with a longitudinal, violet brown to brown stripe. Tentacles with white tip for 1/6 length, violet brown for almost half length, remainder pinkish white with basal 1/5 from eye swollen, with violet brown stripe from eye to base. Siphon and proboscis violet brown to brown.

Radula (Fig. 3F) with central teeth narrow at base; with large, broad, flat heads, outer edge with many perpendicular, sharp cusps, central cusp very large, narrow at base, widening for about half length, where there is usually a lateral denticle on at least one side, then narrowing apically to sharp point; with eight or nine small cusps on either side of central one. First lateral teeth elongate, strongly curved, heads tricuspidate, cusps uneven, central cusp largest. Second lateral teeth elongate, with broad, flat heads, heads with about five long, curved, sharp-tipped cusps.

Egg mass (Fig. 4A) with 57 colourless, transparent, jelly-like capsules laid on a single branch of the host sequentially in an elongated spiral and fused together. Each capsule contains many white-shelled embryos, shells wider than long, shell length 150–230 µm, shell round, punctate with thin operculum (Figs 4B, 4C).

Range: The new material examined here is from northern Spencer Gulf, S. Aust. Cate (1973a) gave the type locality of *P. (P.) heleneae* as the "S. end of St Vincent Gulf, South Australia, (34°55'S 138°10'E)", but the holotype is labelled in Verco's handwriting "G. St Vincent or Spencer Gulf, dredged", so Cate's (1973a) restriction of the type locality is suspect. The range of this species is assumed to be central S. Aust. It is noteworthy that Cotton (1935) refers to the occurrence of *Crenavolva verconis* in southern W.A., but we can find no specimens to substantiate it. Cate (1973a) refers Cotton's (1935) reference to a Queensland species, *Primovula (P.) platysia* Cate, 1973 (as *Ovula formosa* Verco), but does not mention if he examined the specimens.

Habitat: On fans of the gorgonian coral *Euplexaura* sp. (Cnidaria: Octocorallia: Plexauridae), in areas of strong tidal movement.

Remarks: The specific identity of the host coral (SAM H355) could not be determined (P. Alder-Blade pers. comm.). The white spicules (Fig. 5C) are typical of *Euplexaura*. In northern Spencer Gulf, colonies (Fig. 5A) are multi-branched fans in one plane perpendicular to the strong tidal currents, they are attached by a thickened base to a large shell fragment or other piece or pieces of solid debris in the substrate; a poorly sorted, silty, shelly sand. Colonies are relatively large (ca 30 cm high), and widely and irregularly dispersed at 10–20 m depth. Distribution appears to be associated with tidal current velocity and substrate siltiness. *Euplexaura* sp. appears to be less tolerant of silt than *Echinogorgia* sp., and is less common. Each *Euplexaura* sp. colony usually hosts two to five individuals of *P. (P.) heleneae*. Polyps are usually withdrawn during daylight on all of the colony regardless of the presence of *P. (P.) heleneae*. Orientation of the shell is always with the longitudinal axis parallel to the branches of the host, with no observed preference for a head up or head down attitude. No particular position on the host is favoured, and adults and juveniles are present together. Eggs have been observed in late autumn and early winter, laid on a single branch of the host and not attended by the parent, although adults were present on the host.

The colour pattern of the extended mantle lobes of *P. (P.) heleneae* is almost identical to that of *Euplexaura* sp. The background colour of the coral is pastel red, and the withdrawn polyps are red to reddish brown. The pattern of reddish brown patches on the mantle lobes of *P. (P.) heleneae* mimics the position of the polyps on the coral, and an animal with the mantle lobes fully extended is

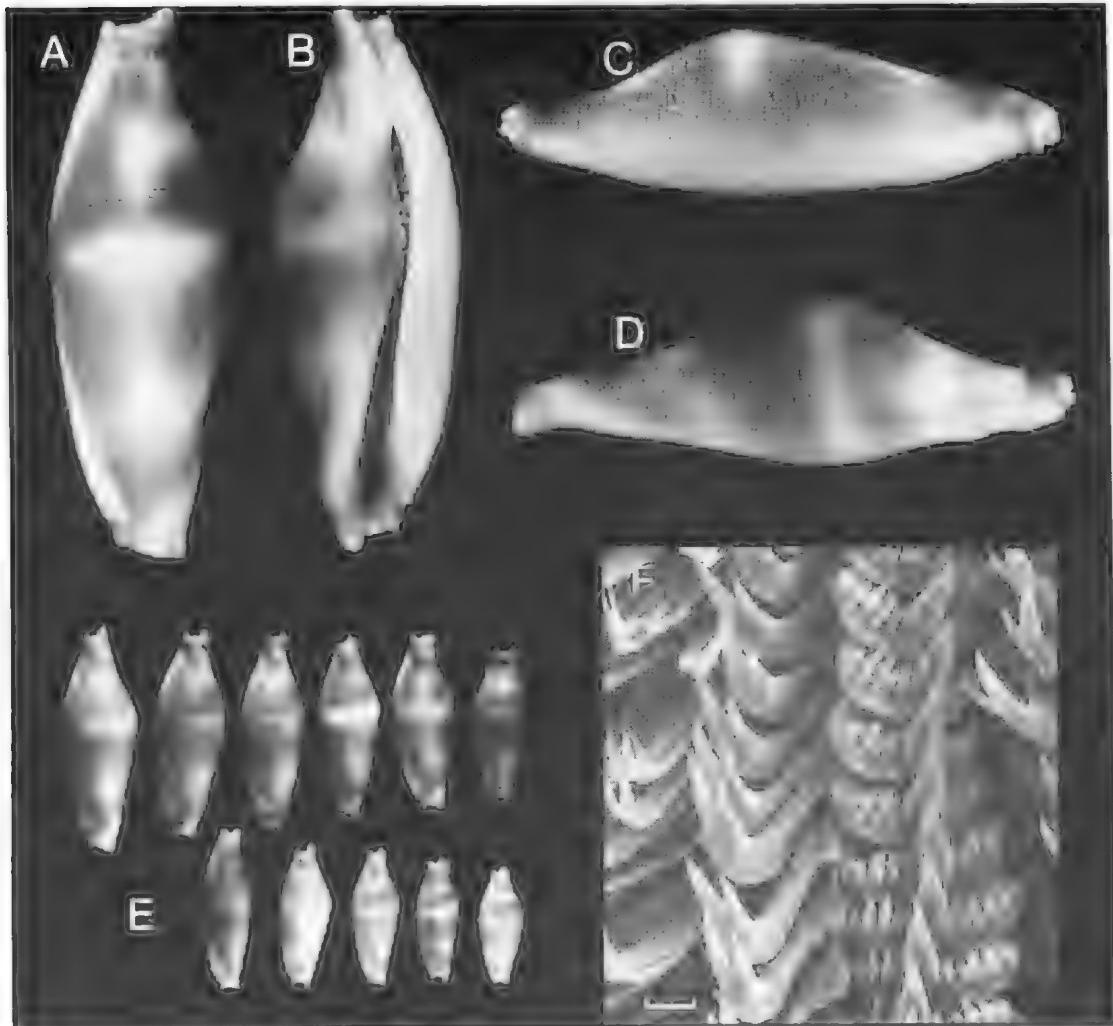


Fig. 3. *Primavula (P.) heleneae* (SAM D17975). A, dorsal view, $\times 7.5$; B, ventral view, $\times 7.5$; C & D, lateral views, $\times 7$; E, size range, $\times 2.5$ (SAM D18434); F, radula, scale bar = $10 \mu\text{m}$ (SAM D17973).

very well camouflaged. The very close mimicry by *P. (P.) heleneae* of its host suggests that it is an obligate predator and that its distribution will be limited by that of *Euplexaura* sp. The distances between colonies of *Euplexaura* sp. (10's of metres) suggest that adults of *P. (P.) heleneae* would not move between colonies, so dispersal is probably by a free-swimming veliger stage of short duration.

Crenavolva cruenta sp. nov.

FIGS 2, 7.

Holotype: SAM D18431, dry adult specimen $10.45 \times 3.60 \times 3.00$ mm, collected on the gorgonian coral *Echinogorgia* sp. at 15 m depth, 1.6 km E. of Douglas Point, northern Spencer Gulf, S. Aust., $32^{\circ}51'48"S$, $137^{\circ}49'12"E$, by N. J. C. Holmes, 5.v.1988.

Paratypes: Same locality data as holotype. Spirit specimens: SAM D18433, 14 juv., 4.65–9.60 mm, 24 ad., 7.35–11.65 mm. Dry specimens: SAM D18432, six juv., 6.30–9.15 mm, 27 ad., 7.15–12.35 mm. SAM D18437, 11 ad., 6.70–12.60 mm. AM CI56094, two ad., 9.55 and 10.90 mm respectively. NTM PI384, two ad., 9.45 and 10.20 mm respectively. NMV F52836, two ad., 9.35 and 9.95 mm respectively. QM MO.19385, two ad., 9.40 and 9.70 mm respectively. TM EI7744, two ad., 9.15 and 9.35 mm respectively. WAM 152/88, two ad., 8.30 and 10.30 mm respectively. NMNZ MF. 49494, two ad., 8.65 and 10.60 mm respectively.

Other material examined: Two broken specimens in spirit from Douglas Bank northwest, northern Spencer Gulf, S. Aust., $32^{\circ}47'18"S$, $137^{\circ}49'12"E$, E. Oks, Sept. 1987 (SAM D17976); Backy Point

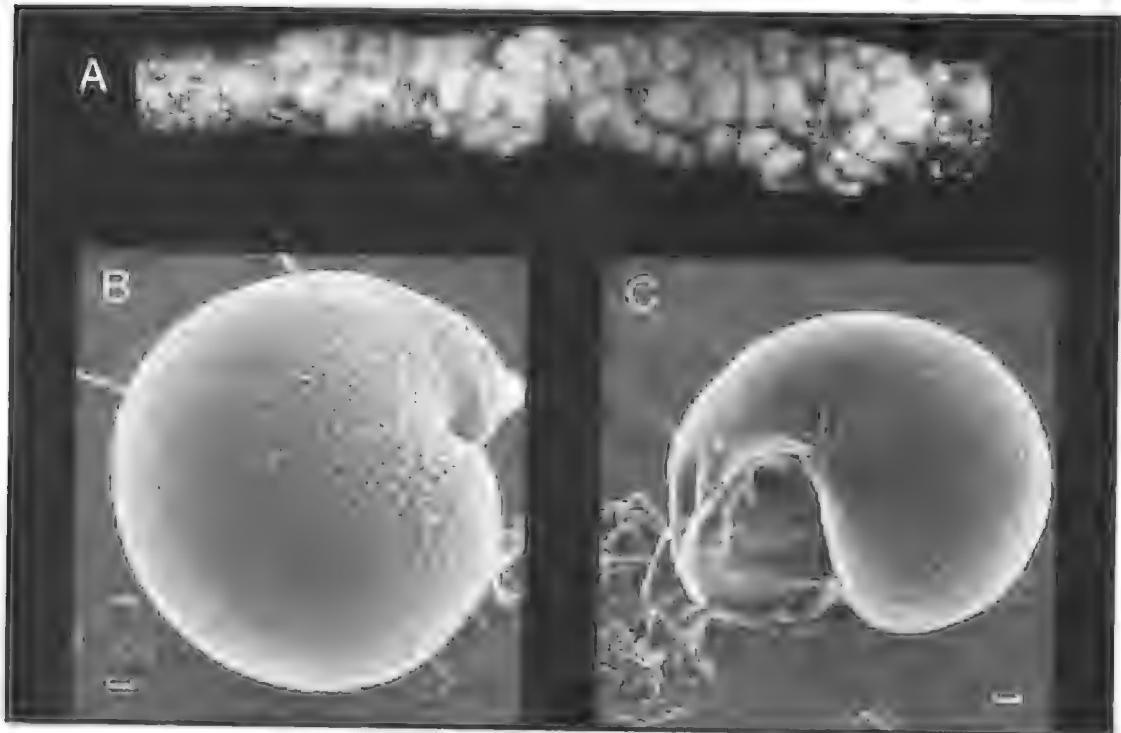


Fig. 4. *Primovula (P.) heleneae* (SAM D17973), A. egg mass on branch of *Euplexaura* sp., $\times 4$; B. embryonic shell, dorsal view; C. embryonic shell, showing aperture and operculum, scale bar = 10 μm .

east, northern Spencer Gulf, S. Aust., $32^{\circ}55'00''\text{S}$, $137^{\circ}51'24''\text{E}$, E. Oks, Sept. 1987 (SAM D17977).

Diagnosis: Small allied cowrie, adult length 6.70-12.60 mm, mean 9.51 mm \pm 1.2. Elongate; both ends produced. Dorsum sculptured with numerous transverse wavy striae; funiculum not prominent; aperture narrow with strong fossula; outer lip outer margin with slight to prominent terminal nodules; both canals bordered by slightly projecting terminal ridges. Shell greyish orange to brownish red; tips red to orange; dorsal bands and patches usually present, white, pale yellow to pale orange; columellar callus, outer lip and labial callus yellow to light orange; fossula pinkish white. Animal mantle lobes translucent pale greyish pink with dark red spots and small and large white papillae; foot ruby, underside with median longitudinal very pale pinkish white stripe; tentacles with white tip for $\frac{1}{4}$ length, remainder of tentacle, siphon and proboscis ruby.

Description of Holotype: (Figs 7A-D) Shell elongate; both ends produced; widest part of dorsum in posterior 2/5. Dorsum sculptured with numerous transverse wavy striae; funiculum not prominent, smooth. Base somewhat concave, outer lip flat, inward sloping; parietal-columellar lip

convex; aperture narrow with a strong fossula, both sides strongly calloused. Parietal-columellar base smooth with faint transverse striae present on central inner part. Outer lip with rounded transverse ridges, becoming weaker anteriorly; inner margin smooth, outer margin with four slight nodules at posterior end, three slight and one prominent nodule at anterior end.

Anterior canal shallow "U"-shaped, slightly flaring, bordered on both sides by distinct and slightly projecting terminal ridges. Posterior canal somewhat produced, shallow "U"-shaped, strongly flaring, bordered on both sides by distinct and slightly projecting terminal ridges, outer lip ridge terminating in a nodule, parietal-columellar lip ridge with two nodules, one terminal.

Shell orange red, anterior and posterior tips bright red; light yellow median band across widest part of dorsum, continuing onto base; light yellow diffuse band midway between median band and posterior end, continuing onto base; light yellow patch almost midway between median band and anterior end. Outer lip and labial callus yellow; columellar callus translucent yellow with dorsal colour pattern visible. Interior of posterior and anterior canals red, becoming orange red at very tips. Fossula pinkish white.

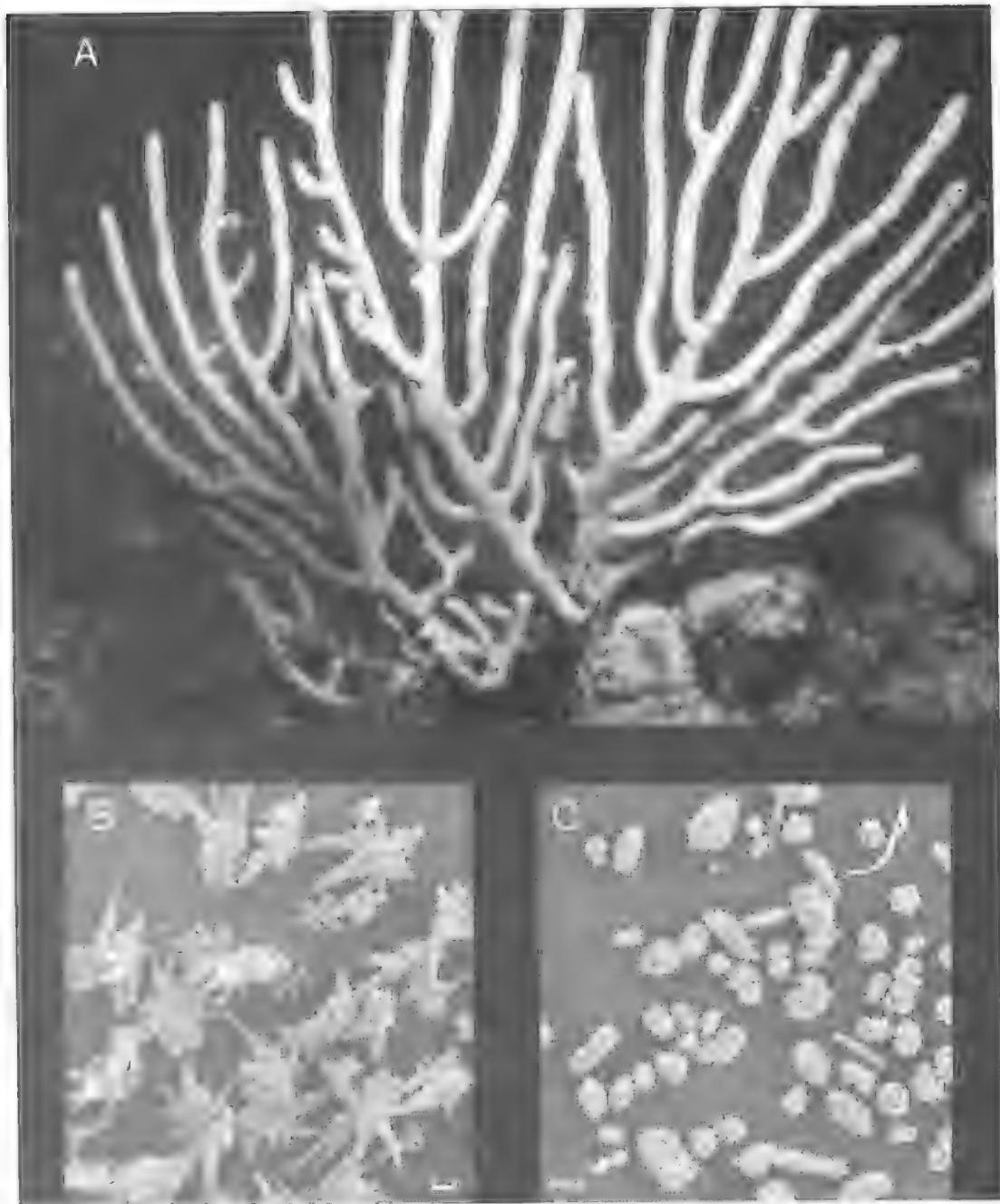


Fig. 5. A. *Euplexaura* sp. colony in situ, $\times 0.8$; B. *Echinogorgia* sp. spicules, scale bar = 100 μm (SAM H356); C. *Euplexaura* sp. spicules, scale bar = 100 μm (SAM H355).

Etymology: "Cruentus" (L.) meaning bloody, pertaining to the main colour of the shell and the animal.

Additional Characters from Paratypes: Animal mantle (Fig. 2) lobes translucent pale greyish pink

with random, dark red spots, rows and groups of small, simple white papillae and occasional much larger, white, elevated, rounded papillae with wart-like knobs, mantle more opaque white at base of papillae. Foot uniform ruby, underside of foot with median, longitudinal, very pale pinkish white stripe;



Fig. 6. *Echinogorgia* sp. colony *in situ*, $\times 0.75$.

anterior dorsal foot with series of prominent, vertical lamellae, becoming less distinct posteriorly, disappearing about $\frac{1}{3}$ length of foot from anterior end. Tentacles with white tip for $\frac{1}{4}$ length, remainder ruby with basal $\frac{1}{6}$ from eye swollen. Siphon and proboscis ruby.

Radula (Fig. 7F) with central teeth narrow at base, with large, broad, flat heads, outer edge with many perpendicular, sharp cusps, central cusp very large, tapering apically to sharp point, with sharp, lateral denticle on either side at about half length; with five or six small cusps on either side of central one.

First lateral teeth elongate, strongly curved, heads tricuspidate, cusps uneven, central cusp largest. Second lateral teeth elongate with broad, flat heads, heads with eight long, curved, sharp-tipped cusps

Variation: Paratypes differ from the holotype in size, shell colour and sculpture (Fig. 7E). Shell colour is from greyish orange to brownish red; anterior and posterior tips red to orange; dorsal bands and patches white, pale yellow to pale orange, and vary from very prominent (often forming three distinct bands) to almost absent, median band being most conspicuous; columellar callus, outer lip and labial callus yellow to light orange.

Funiculum varies from smooth to with up to five weak nodules on inner edge. Outer lip outer margin nodules vary from very slight with one prominent nodule at anterior end, to three prominent nodules at posterior and two prominent nodules at anterior end. Posterior end usually much more produced in small specimens, almost rostrate. Posterior canal parietal-columellar lip ridge occasionally with three or four nodules.

Range: Northern Spencer Gulf, S. Aust.

Habitat: On fans of the gorgonian coral *Echinogorgia* sp. (Cnidaria: Octocorallia: Paramuriceidae), in areas of strong tidal movement.

Comparison with other species: The new species belongs in *Crenavolva*, which is distinguished from other genera in the Ovulidae by the small, elongate shell with median angulation, narrow, produced but truncate ends, dentate, curved aperture, striate dorsum and ridged outer lip (Cate 1974). *C. cruenta* most closely resembles *C. striatula* (Sowerby, 1828) and *C. verconis*, the congeners recorded from Australia. Cate (1973a) records two subspecies from Australia, *C. s. traillii* (A. Adams, 1855) and *C. s. tinctura* (Garrard, 1963), both from Queensland. *C. cruenta* can be distinguished from *C. striatula* and *C. verconis* by its narrower, more elongate form, more produced ends, the shape of its more elongate aperture, and shell colour pattern.

Remarks: The specific identity of the host gorgonian coral (*Echinogorgia*: P. Alderslade pers. comm. SAM H356) could not be determined; the red thorn scale spicules (Fig. 5B) are typical for the genus. In northern Spencer Gulf, colonies of this species (Fig. 6) are sparsely branched fans in one plane, attached by a slightly thickened base to shells, fragments or pebbles in the substrate; a poorly sorted, silty, shelly sand. Colonies are relatively small (ca 15 cm high), and appear much more tolerant of silt than *Euplexaura* sp., being widely

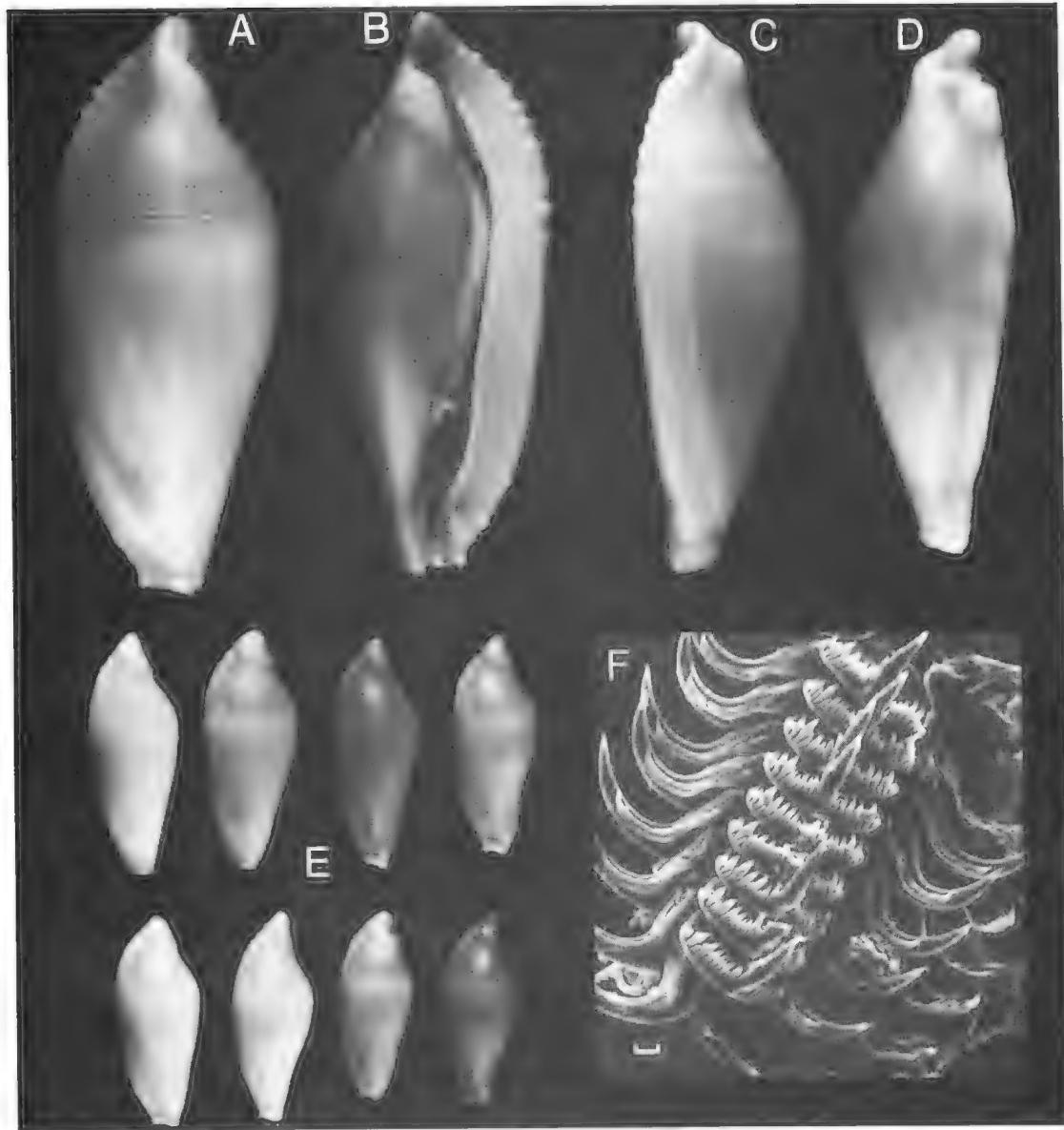


Fig. 7. *Crenavolva cruenta* sp. nov. holotype (SAM D18431), A. dorsal view, $\times 6.6$; B. ventral view, $\times 6.6$; C & D. lateral views, $\times 6.6$; E. size and colour pattern range, paratypes, $\times 2.25$ (SAM D18437); F. radula, paratype, scale bar = $10 \mu\text{m}$ (SAM D18433).

but patchily distributed in 10–20 m of water, often in quite high densities (up to 20 colonies/m²). When *C. cruenta* is present, each *Echinogorgia* sp. colony usually hosts one to three individuals. From observations made in daylight, the host's polyps are usually withdrawn on all or most of the colony when *C. cruenta* is present. Orientation of the shell is always with the longitudinal axis parallel to the branches of the host, with no observed preference for a head up or head down attitude. No particular

position on the host is favoured, and adults and juveniles are present together.

Colour pattern and form of the extended mantle lobes of *C. cruenta* are almost identical to *Echinogorgia* sp. The background colour of the gorgonian coral is red: the polyps are reddish orange when withdrawn, yellow when extended. The thorn scale spicules in *Echinogorgia* sp. protrude through the surface of the colony, giving it a rough texture. These protruding spicules help retain a ragged layer

of mucus and detritus upon the surface; this mucous layer is white, and patchily masks the red background colour. The pattern of reddish brown patches and white papillae on the mantle lobes of *C. cruenta* mimics the ragged mucus on the gorgonian coral, and an animal with the mantle lobes fully extended is very well camouflaged on its host. The very close mimicry of *C. cruenta* to its host suggests that it is an obligate predator and that its distribution is limited by that of *Echinogorgia* sp. The distances between colonies of *Echinogorgia* sp. (often <0.5 m) and the suitability of *C. cruenta*'s camouflage suggest that the latter would be able to move across the substrate between colonies, so dispersal is probably only partly by a free-swimming veliger.

Discussion

The generic names used in this paper follow the system and modifications proposed by Cate (1973a, 1973b, 1974). The distinctions between some of the genera used there are inadequate.

The two species of Ovulidae previously named from S. Aust.: *Crenavolva verconis* and *Primovula (*P*) heleneae*, are both based on damaged, dead shells. Verco (1908) had three specimens and recorded them as *Ovula formosa* A. Adams & Reeve, 1848, a species described from Borneo. The description and photographs of the holotype of *O. formosa* [= *Delonovula formosa* (A. Adams & Reeve, 1848)] in Cate (1973a) were compared with the holotype of *C. verconis*, with the holotype and other specimens of *P. (*P*) heleneae*, and with the types of *C. cruenta* and *D. formosa* was found to differ significantly from them. *D. formosa* is bright purple with yellow tips; the lassula is not prominent; the whole shell is much narrower overall, with a narrower outer lip than either *C. cruenta*, *C. verconis* or *P. (*P*) heleneae*; and a more pointed posterior tip than either *C. cruenta* or *C. verconis*, and which lacks the basally projecting terminal knob of *P. (*P*) heleneae*.

Cotton & Godfrey (1932) described Verco's specimens as a new species, *Prosimnia verconis*. Their description obviously was based on all the specimens, although the holotype is clearly defined as the shell from St Francis Island (SAM D13476, = D10174). Cate (1973a) re-examined the types of *P. verconis*, which now consisted of two specimens, (one specimen of the original series is missing, presumed lost), and discovered that they were not conspecific. Cate acknowledged the designation by Cotton & Godfrey (1932) of the specimen registered SAM D13476 (= SAM D10174) (very worn and faded), as the holotype of *Crenavolva verconis* (Cotton & Godfrey, 1932), and used Cotton & Godfrey's (1932) paratype (SAM D15943); a worn, faded and broken specimen, as the holotype of *Primovula (*P*) heleneae*. The live collected material from upper Spencer Gulf was compared with the types of both species and, although both types are damaged, the material collected from *Euplexaura* sp. was clearly conspecific with *P. (*P*) heleneae*, and all of the new material was different from the designated holotype of *C. verconis*.

According to Coleman (1981), the specimen illustrated by Coleman (1975, fig. 262) as *Neosimnia verconis* (Cotton & Godfrey, 1932) is actually a specimen of an unnamed species of *Acyvolva*.

Acknowledgments

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DEVELOPMENTAL BIOLOGY OF THE AUSTRALOPAPUAN HYLID FROG LITORIA EUCNEMIS (ANURA: HYLIDAE)

*BY MARGARET DAVIES**

Summary

The egg mass and tadpole stages of *Litoria eucnemis* are adapted for a stream-dwelling habit. The egg mass is compact and adherent whilst the tadpoles have suctorial mouthparts and shallow fins. The eggs have a large yolk reserve used by the tadpole for nutrition between stages 19 and 26 after hatching. At 16-24°C, *L. eucnemis* metamorphoses 74 days after egg laying and 69 days after hatching.

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DAVIES, M. (1989) Developmental biology of the Australopapuan hylid frog *Litoria eucnemis* (Anura: Hylidae). *Trans. R. Soc. S. Aust.* 113(4), 215-220, 30 November, 1989.

The egg mass and tadpole stages of *Litoria eucnemis* are adapted for a stream-dwelling habit. The egg mass is compact and adherent whilst the tadpoles have suuctorial mouthparts and shallow fins. The eggs have a large yolk reserve used by the tadpole for nutrition between stages 19 and 26 after hatching. At 16-24°C, *L. eucnemis* metamorphoses 74 days after egg laying and 69 days after hatching.

KI1 WHIRLS: *Litoria eucnemis*, tadpoles, developmental biology, lotic adaptations

Introduction

Litoria eucnemis (Jönnberg) is distributed in rainforest streams at widely-separated localities in New Guinea (Tyler 1968; Zweifel 1980) and on the Cape York Peninsula in northern Queensland (Zweifel 1980; Cogger 1986). The species has had an unstable nomenclatural history in Australia (Tyler & Watson 1985) and the names *Litoria eucnemis*, *L. serrata* and *L. gemmaculata* have variously been applied to Australian representatives of the species.

Life history data are confined to a comment that the eggs are dark brown and that nothing appears distinctive about the tadpole (Menzies 1974).

A pair of *L. eucnemis* bred in the laboratories of the Zoology Department, University of Adelaide. The tadpoles were reared to metamorphosis and the development of the species is reported here.

Materials and Methods

Specimens of *L. eucnemis* were collected by M. Mahony, J. Read, M. Schmidt and T. Haff at Charnmillin Ck, Qld (17°43' 145°31') in late August 1988 and reached Adelaide on 1.ix.1988. A pair of frogs, amplexant upon arrival, was transferred to a glass aquarium with a pond of water at one end. The aquarium was maintained at room temperature.

Spawn was removed from the pond, and placed in dechlorinated, aerated tap water in a glass aquarium 25x25x8 cm for 24 hr at 30°C. The aquarium was then maintained at room temperature, aerated and the water changed daily. Tadpoles were fed on lightly-boiled lettuce leaves. The culture was divided in two on 26.x.1988. To give the tadpoles rough surfaces on which to attach, alga-covered stones were introduced to the aquaria when the spawn hatched.

Samples of embryos and larvae were collected as shown in Table I and preserved in Tyler's fixative (Tyler 1962).

Measurements of developmental stages were taken using vernier callipers reading to 0.05 mm. Illustrations were made with the aid of a Wild M8 stereodissecting microscope and camera lucida.

Developmental stages were classified according to Gosner (1960).

Results

Amplexus: Amplexus was axillary (Fig. 1). The pair was amplexant upon arrival in the laboratory possibly in response to the reduced air pressure in the cargo hold of the aeroplane (M. J. Tyler & M. Davies unpubl. obs.).

Eggs: Oviposition took place overnight, 2 and 3.ix.1988. Temperature of the water in which the eggs were laid was 18.5°C. The egg mass of 843 eggs was 67.5 mm at its greatest width and compact. Individual jelly capsules were tightly adherent to each other (Fig. 2). The animal pole was dark brown and approximately half of each egg on the vegetal hemisphere was white. Only one membrane was detected in each capsule.

Mean diameter of six eggs was 2.25 mm (range 2.10-2.56 mm) and of the capsules, 2.98 mm (range 2.60-3.60 mm). On the day following oviposition, the eggs were in late cleavage (Stage 9). Within 24 hours they had progressed to the neural fold stage (Stage 14) and within a further 24 hours, the embryos were at Stage 17. The embryos were perched on a large chocolate-coloured yolk sac (Fig. 3); large crescentic adhesive organs were located anterodorsally. A prominent stomodaeal pit was located posterodorsally to the adhesive organ (Fig. 3).

On 7.ix.1988, the embryos remained in the jelly capsules. The adhesive organs were beginning to divide as head flexion commenced. The stomodaeal notch was prominent and the pronephros was apparent laterally; the gill plate was clearly

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delineated. The tail was differentiated and the embryos were at Stage 18.

Larvae: The embryos hatched on 8.ix.1988 at Stage 19. The head was flexed ventrally and the adhesive organs situated ventrolaterally as two raised pigmented suckers. A stomodaeal depression was dorsomedial to the suckers. The primordia of two pairs of gill filaments were present and eye bulges were apparent (Fig. 4a). The pronephros was

still apparent. A large yolk sac provided nutrition for the embryo.

By 9.ix.1989 the embryos were at Stage 20. The two pairs of gills were now filamentous, the anterior pair with four to five branches, the posterior pair with one to three. Ventral suckers were ventrolateral to an open mouth. The optic bulges were well developed but opaque. Nutrition was supplied by a large yolk sac (Fig. 4b).

TABLE 1. Dimensions of developmental stages of *Litoria euthemis*.

Age (days, date)	Stage	Body length \bar{x} , range in parentheses (mm)	Total length \bar{x} , range in parentheses (mm)	n
6 (8.ix.1989)	19	3.12 (2.96-3.18)	5.07 (4.95-5.25)	6
7 (9.ix.1989)	20	3.43 (3.3-3.5)	6.6 (6.4-6.8)	3
8 (10.ix.1989)	20	3.47 (3.25-3.9)	8.03 (7.8-8.2)	3
9 (11.ix.1989)	21/22	3.65 (3.4-4.05)	8.68 (8.0-9.4)	12
12 (15.ix.1989)	24	4.04 (3.6-4.3)	10.96 (9.9-12.0)	16
14 (17.ix.1989)	25	4.35 (3.9-4.8)	12.3 (11.0-13.2)	13
23 (27.ix.1989)	26	5.58 (5.2-6.1)	17.07 (16.1-18.1)	10
31 (5.x.1989)	27	5.57 (5.1-6.0)	16.8 (16.7-17.0)	3
42 (26.x.1989)	30	8.1	23.2	1
42 (26.x.1989)	31	7.92 (7.6-8.4)	24.5 (24.1-25.2)	5
42 (26.x.1989)	32	9.15 (8.8-9.5)	27.3 (26.0-28.5)	2
42 (26.x.1989)	33	9.3	27.9	1
42 (26.x.1989)	34	9.1 (8.7-9.6)	28.9 (27.0-30.8)	3
50 (3.xi.1989)	34	8.98 (8.7-9.2)	27.5 (26.5-27.9)	4
50 (3.xi.1989)	35	9.85 (9.7-10.0)	28.1 (27.5-28.7)	2
50 (3.xi.1989)	36	10.4 (10.3-10.5)	33.7 (33.5-33.9)	2
54 (7.xi.1989)	36	9.65 (9.3-10.0)	30.3 (29.3-31.3)	2
54 (7.xi.1989)	39	9.7 (9.4-10.1)	29.6 (28.0-31.2)	2
54 (7.xi.1989)	40	11.1	34.6	1
57 (10.xi.1989)	41/42	9.8	29.6	1
58 (11.xi.1989)	42	10.6	31.2	1
61 (14.xi.1989)	43	11.8	32.1	1
61 (14.xi.1989)	45	10.5	14.0	1
63 (16.xi.1989)	46	10.2	-	2

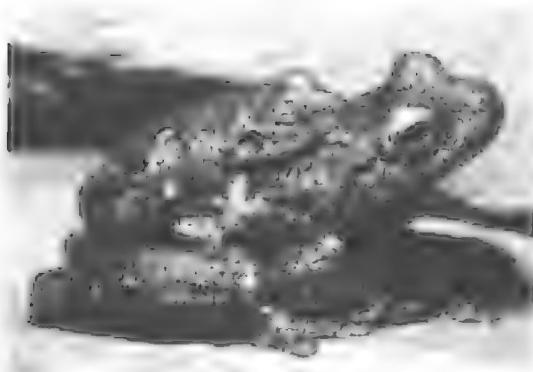


Fig. 1. Amplexant pair of *Litoria eucnemis*.

By 10.ix.1988, the larvae remained at Stage 20 but olfactory pits were now clearly visible. Larvae had reached Stage 21 within the next 24 hours. The cornea was transparent, pigmentation of the adhesive organs was fading and the gills were more filamentous (Fig. 4c). Ridges could be distinguished on the lateral and posterior margins of the mouth, foreshadowing the labial teeth and papillae. The tail had elongated; nutrition was still supplied by yolk.

By 15.ix.1988, the external gills were completely covered on both sides by the operculum. The adhesive organs were degenerating, although some pigmentation remained. The horny beak was keratinized, but the tooth rows had not yet formed. Nutrition was still provided by yolk and the embryo was at Stage 24. Some tadpoles were now free swimming.



Fig. 2. Dorsal view of a spawn clump of *Litoria eucnemis*. Greatest diameter is 67.5 mm.

The spiracle had begun formation by 17.ix.1988. It was situated ventrolaterally and the opening directed posteriorly. Two upper and the two lower entire tooth rows were keratinized. The gut was loosely coiled but yolk-filled, and embryos were at Stage 25.

Larvae were not sampled again until 27.ix.1988. The spiracle had elongated and its orifice was now directed posterodorsally. Mouthparts were complete, the larval gut had formed and the tadpoles were feeding on vegetable matter. The development of the limb buds indicate that the tadpole was at Stage 26.

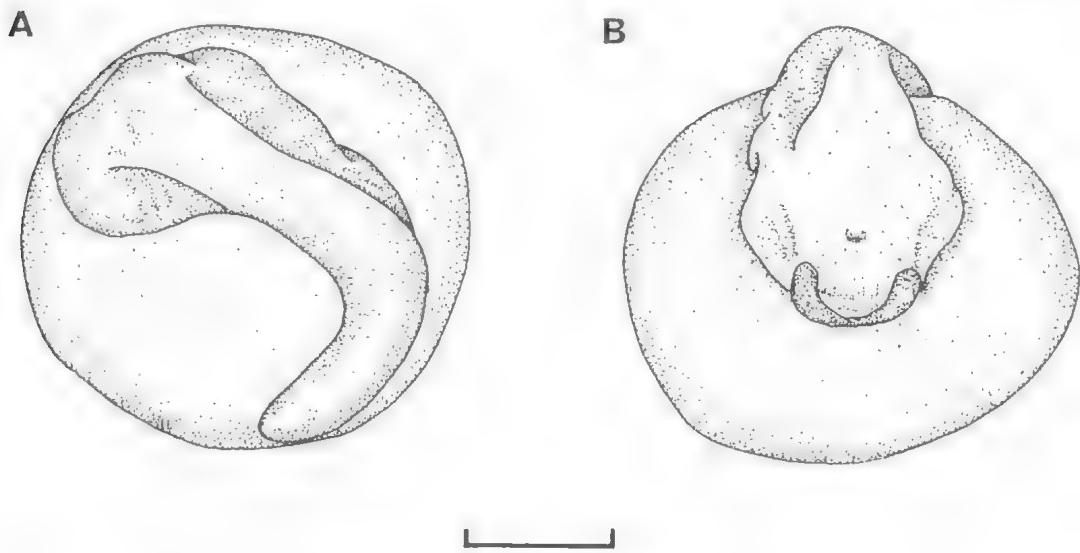


Fig. 3. A) Dorsal and B) anterior views of embryo of *Litoria eucnemis* at Stage 17. Scale bar represents 1 mm.

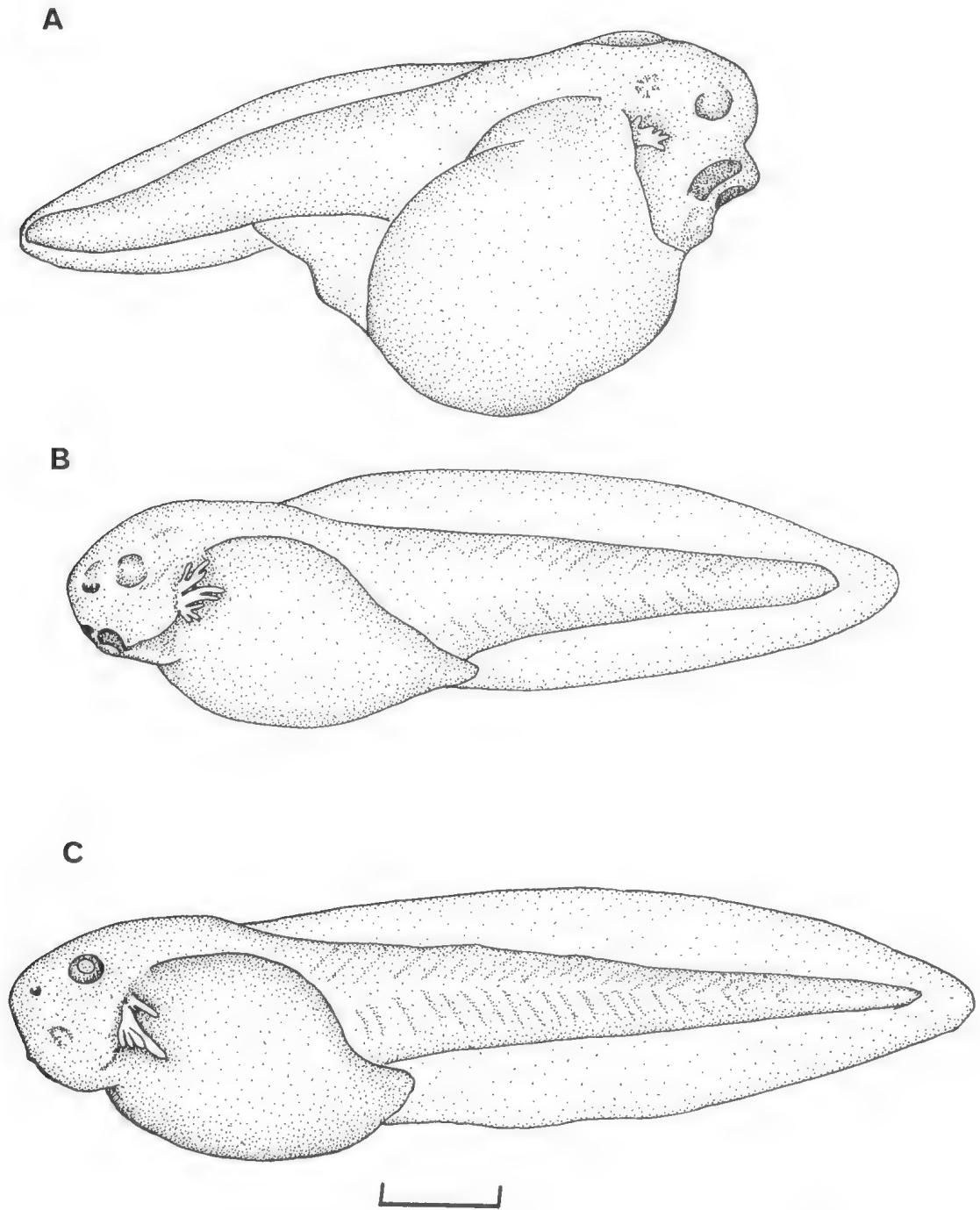


Fig. 4. *Litoria eucnemis* larvae: A) lateral view at hatching, Stage 19; B) lateral view Stage 20; C) lateral view Stage 21. Scale bar represents 1 mm.

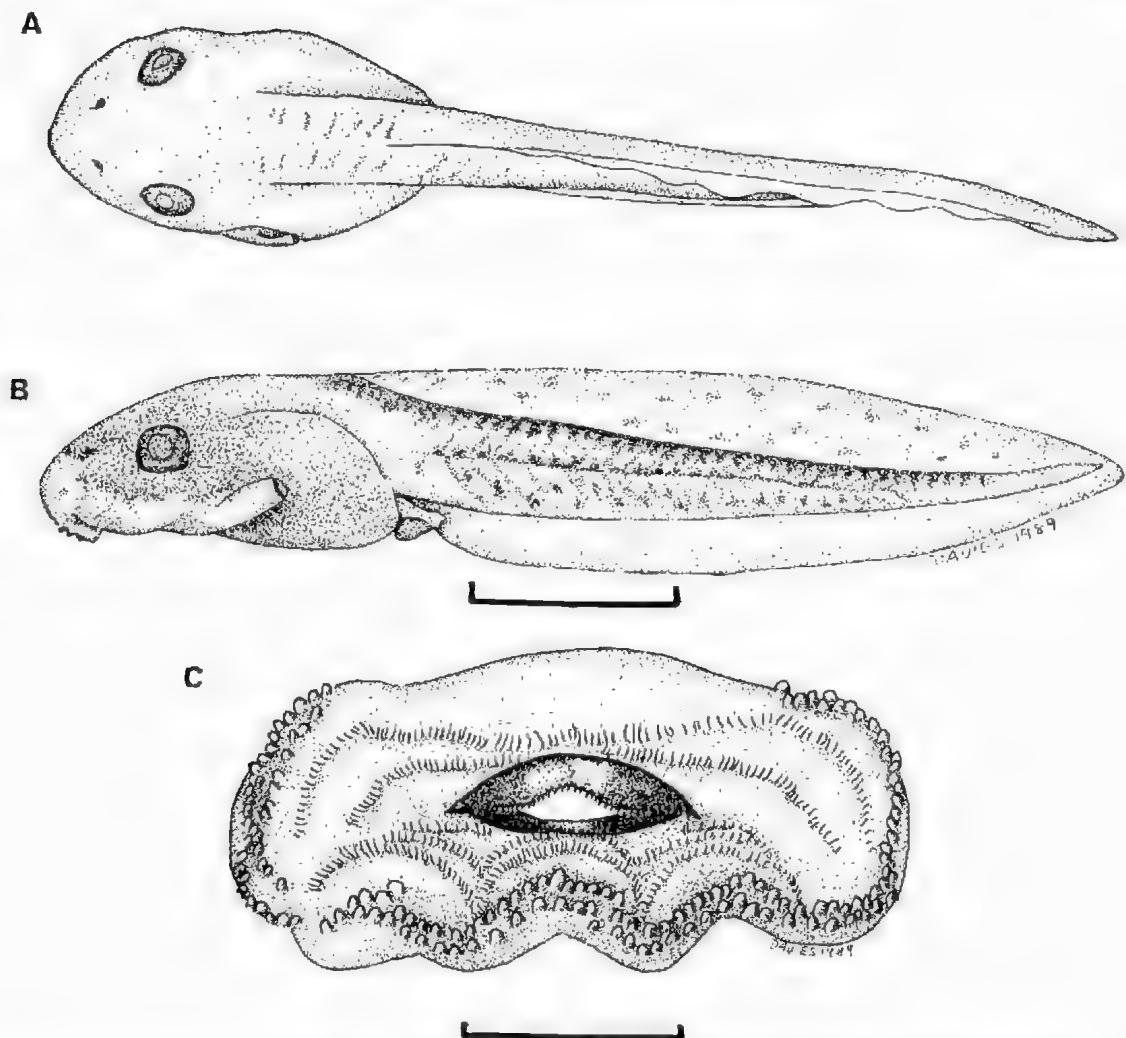


Fig. 5. A) Dorsal and B) lateral views and C) mouth disc of a larva of *Litoria eucnemis* at Stage 31. Scale bar represents 5 mm (A,B) and 1 mm (C).

The next sample of larvae, taken on 5.x.1988, was at Stage 27. The body of the larva was covered with brown pigment dorsally, and was pale ventrally. A disrupted line of pigment granules bordered the dorsal myotomes and further pigment granules were scattered laterally and on the dorsal fin.

Dimensions of developmental stages of *L. eucnemis* are shown in Table 1. A larva at Stage 31 preserved on 26.x.1988 is illustrated in Fig. 5a,b. The anus was dextral and the spiracle elongate and sinistral. The dorsal fin was shallow and tapered to a gently-rounded tip. General body colour was brown with faint pigment granules on the tail myotomes and the dorsal fin.

The mouth disc of a larva at Stage 31 is shown in Fig. 5c. There are two upper and three lower rows

of labial teeth. Both the second upper and the first lower row of teeth have a median gap. There are two rows of labial papillae forming a wide band around the lateral and posterior margins of the mouth.

Metamorphosis: By 10.xi.1988, the left forearm had protruded in one larva and the first froglet at Stage 46 was recorded on 16.xi.1988, a total of 74 days after the eggs were laid and 69 days after hatching. Water temperatures varied throughout the period of development from 16.4–23.8°C.

Larval behaviour: Larvae frequently aggregated, mostly beneath the stones within the aquaria or on the surface of the lettuce. They attached themselves by their suctorial mouthparts to the floor of the aquaria during water changing.

Discussion

The development of *Litoria eucnemis* is unusual amongst Australian hylids in utilising a large yolk reserve and showing relatively late development of the larval gut (the species hatches at stage 19 but the gut does not form until stage 26, 9-19 days after hatching). Such development is more representative of direct-developing species or those that spend a considerable period of their development within the egg capsule [e.g., *Kyarramus sphagnicola* (Moore 1961; Anstis 1981)]. Amongst Australian species, this mode of development is restricted to leptodactylid frogs. *L. eucnemis* is a New Guinea species that extends its range into Australia, and its relationships lie with the new Guinean hylid fauna, in particular the montane species of *Litoria* and *Nectimystes*. Such species lay large unpigmented eggs; tadpoles, where known, exhibit lotic adaptations (Menzies 1974; Tyler & Davies 1979; Zweifel 1983). However, complete life history data are unknown for these species. The eggs of *L. eucnemis* are large in comparison with other Australian hylids (see Tyler 1989 for review), directly related to the mode of early development. [Montane New Guinea *Litoria* and *Nectimystes* species also are described as having large eggs (Menzies 1974)].

The single adherent egg mass is an adaption in *Litoria eucnemis* to a lotic lifestyle; the tooth rows and other structures are typical of other Australian hylids (Martin & Watson 1971), but the suetorial mouth disc is an adaption to fast-flowing waters.

Amongst Australopapuan anurans, there are several kinds of lotic adaptations of the mouth disc. The extreme elaborations exhibited by *Litoria nannospila*, *L. rheneola* (Liem 1974), *L. urukumana* (Menzies 1974), and *Nectimystes thayi* (see Tyler 1989 for Plate) consist of a large suetorial structure occupying the entire ventral preocular region of the tadpole. *Taudactylus* spp have umbrella-shaped lips hanging ventrally (Liem & Hosmer 1973) whilst in *L. subplandulosa* the mouthparts form a funnel in which all labial tooth rows and pigmentation of the horny beak are absent. Oral disc tubercles have keratinised tips whilst unusual black filaments are suspended anteriorly to the pharynx (Tyler & Anstis 1975). The less elaborate adaptations occupying a lesser proportion of the ventroventral surface of the tadpole and exhibited by *L. eucnemis* are shared by *L. caplandi* and *L. meiriana* (Tyler et al. 1983), *L. lesueuri* (Martin & Watson 1971), *Megistophryne ligurius* (Tyler et al. 1979) and *Mixophyes bathus* (Watson & Martin 1973).

Other torrent adaptations include the narrow tail fins and the ventrolateral spiracular opening.

Acknowledgments

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**HYBRIDISATION OF *LITORIA CHLORIS* AND *L. XANTHOMERA*.
(ANURA: HYLIDAE)**

BY GARY R. BEARDSELL

Summary

BRIEF COMMUNICATION

HYBRIDISATION OF *LITORIA CHLORIS* AND *L. XANTHOMERA*. (ANURA:HYLIDAE)

A study of intraspecific variation among the three disjunct populations of *Litoria chloris* (Boulenger) of Eastern Australia showed that the northern population differed in morphology from the other two populations¹.

Isoenzyme electrophoresis demonstrated extensive genetic divergence between the northern and southern populations resulting in the recognition of the northern population as a distinct species, *L. xanthomera*².

Early development and larval morphology of *L. chloris* have been described¹ and the larvae of *L. xanthomera* are identical to those of *L. chloris*².

Here I test genetic compatibility through a fertile cross between a captive male *L. chloris* and a female *L. xanthomera*.

Two adult male *L. chloris* were acquired from Finch Hatton Gorge, Mackay, Queensland in January 1984, and one adult female of *L. xanthomera* from Crystal Falls near Cairns, Qld on 10.xii.1987. The frogs were housed in an indoor terrarium. Amplexus occurred on 28.i.1988.

Embryos were reared in an aquarium with rainwater to a depth of 24 cm. Water temperature was 18–29°C. Larvae were fed pond algae, commercial fish food and boiled lettuce. When they approached metamorphosis they were transferred to a terrarium. The froglets were fed on house flies and flour moths.

Measurements were made using vernier calipers reading to 0.1 mm and an ocular micrometer to 0.1 mm. The larval mouth disc was drawn under a stereoscopic microscope while the larval and froglet drawings were inked directly onto enlarged photographs, that were later treated with potassium iodide and a sodium thiosulphate fixing bath to remove the photographic image and iodine stain respectively¹. Developmental stages follow Gosner³.

Calling commenced on 17.xi.1987 and continued on most nights through to mid-January when the female *L. xanthomera* became gravid. Amplexus occurred on

28.ii.1988 at 0800 hr, and the male continued to call for one minute while the female produced a soft call. The amplexant pair was then placed into a smaller breeding aquarium.

Oviposition occurred from 0630 to 0700 hr on 29.ii.1988. Approximately 600 eggs were laid as a flat, jelly-like mass on the surface of the water; mean ovidiameter = 1.5 mm, capsule diameter = 4.4 mm, (n = 6). The animal pole was dark brown, the vegetal white. The fertile eggs began to sink and adhere to the bottom and sides of the aquarium in the first hour.

Dimensions of the embryos and larvae are shown in Table 1. Hatching began 1.iii.1988 at stages 20 & 21. The embryos were dark to mid brown; length: 6.5 mm. Each embryo had three pairs of external gills with numerous branches.

On 3.iii.1988 the larvae were at stage 23. The operculum developed and melanophores appeared along the mid-dorsal line, over the tail musculature and as circular patches over the dorsal surface of the abdomen. The larvae were pale brown and the coils of the intestines visible through the abdominal wall. The larvae reached stage 25 at 1700 hr (4.iii.1988).

At stage 29 (Fig. 1A) the larvae had a total length of 15.5 mm and a body length of 5 mm. Most larvae developed a lateral curvature of the tail of varying degrees of severity between stages 28–30 in weeks 4 & 5. At this point there was marked variation in growth: some larvae attained a total length 2x that of others. As the larvae approached stages 34–38 between weeks 5 and 7 the severity of the tail bend increased into an S-shape in many individuals (Fig. 2). At stage 34 body colour was light brown with a transparent area over the abdominal wall. Pigmentation was apparent on the dorsal tail fin and tail musculature (Fig. 1B). On day 49 the largest larva measured 52 mm in stage 40 (Fig. 1C).

The mouth disc (Fig. 3) of a larva in stage 34 has the typical hylid formula of

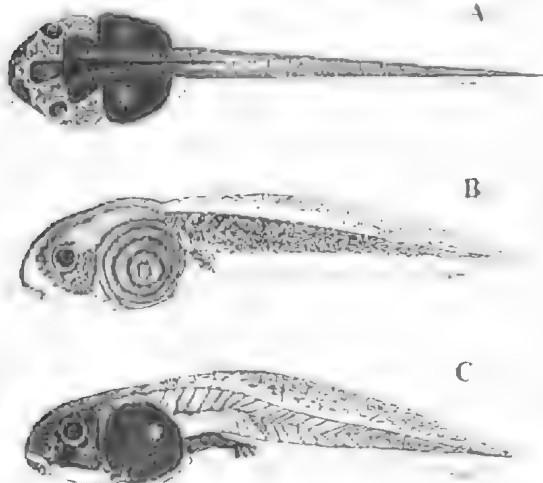


Fig. 1. Developmental stages of a fertile cross between *Litoria chloris* and *L. xanthomera*. A, Stage 29; B, Stage 34; C, Stage 42. Scale bar = 1 mm.



Fig. 2. Abnormal tail bend in a hybrid larva at Stage 40. Total length 52 mm.

TABLE 1. Dimensions of developmental stages of a cross between *Litoria chloris* and *L. xanthomera*.
Means (mm) with ranges in parentheses

AGE (Hours)	STAGE	SAMPLE (N)	EMBRYO DIAMETER	CAPSULE DIAMETER	BODY LENGTH	TOTAL LENGTH
0	2	6	1.5 (1.5-1.6)	4.5 (4.3-4.7)	—	—
1.5	3	—	—	—	—	—
2.75	4	—	—	—	—	—
3.75	8	—	—	—	—	—
6	10	—	—	—	—	—
10.75	10 & 11	—	—	—	—	—
11.75	11	—	—	—	—	—
12.5	12	—	—	—	—	—
15	13	—	—	—	—	—
(Days)						
1	18	5	4.4 (4.2-4.8)	—	—	—
2	21	6	6.5 (5.9-6.9)	—	—	—
3	23	5	7.1 (7.0-7.3)	—	—	—
4	25	5	7.9 (7.7-8.0)	—	—	—
8	26	5	—	—	4.3 (4.1-4.4)	10.3 (9.8-10.6)
37	33	4	—	—	12.1 (10.2-12.3)	38.2 (36.7-39.1)
38	38	4	—	—	13.4 (13.1-13.7)	39.3 (38.9-39.9)
45	40	3	—	—	22.4 (21.6-22.7)	52.1 (50.1-52.8)
51	46	4	—	—	14.7 (14.4-15.1)	52.1 —

In many larvae extra papillae with labial teeth appeared between the upper rows of labial teeth (Fig. 3).

Four froglets completed metamorphosis 20.iv.1988 and had snout-vent (S-V) lengths of 14.4, 14.6, 14.8 and 15.1 mm. The remaining 52 surviving larvae completed metamorphosis by 26.iv.1988. The majority of juveniles metamorphosed with pelvic girdle abnormalities (Fig. 4A) to varying degrees of severity. Approximately one third of the juveniles displayed no external sign of skeletal abnormalities (Fig. 4B). The colour of juveniles was mid-

brown with a very fine, diffuse speckling of white disappearing after one week.

The embryo and larval lifespan extended over a period of 51-56 days at 18-29°C. The froglets were measured at monthly intervals after completion of metamorphosis (Fig. 5). Within a few days they developed a white supralabial stripe disrupted in some individuals and complete in others. The mid-brown colour changed to a light mustard-brown within two weeks of metamorphosis. By 5.v.1988

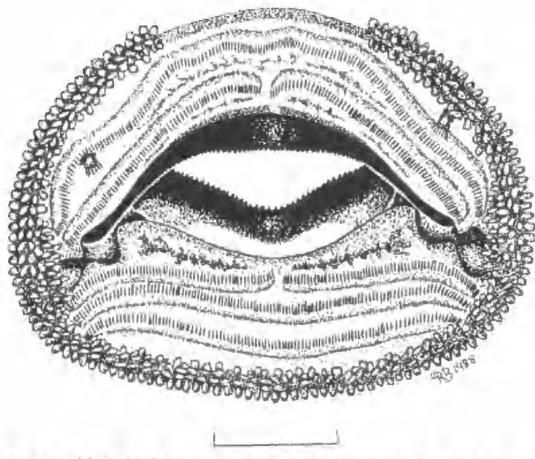


Fig. 3. Hybrid larval mouth disc at Stage 34. Scale bar = 1 mm.

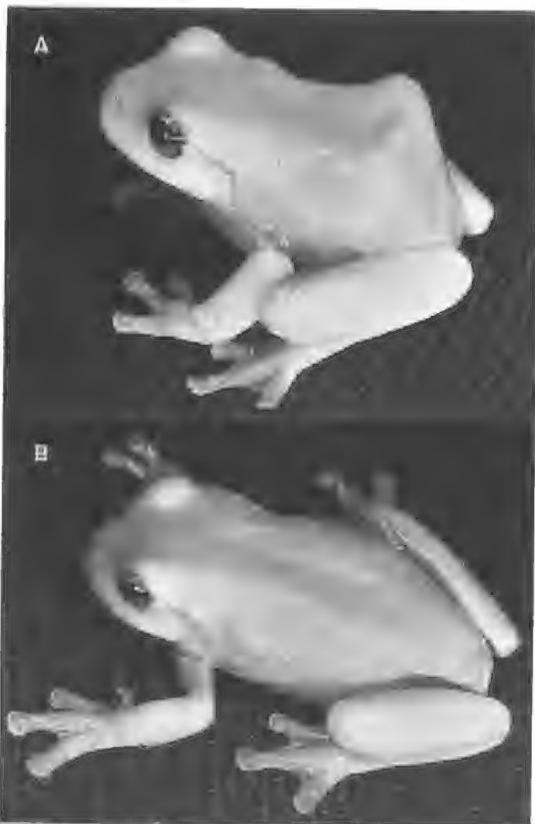


Fig. 4. A, Pelvic girdle abnormalities in a three month old hybrid froglet (S-V 23 mm); B, Normal three month old hybrid froglet (S-V 27.2 mm).

the supralabial stripe developed a green tinge while green pigmentation developed on the supraorbital skin.

The thighs developed the orange of *L. xanthomera* by May–mid June, the supralabial stripe became indistinct concomitantly, with a green tinge over the brown on the body parts that are green in the adult life. After eight months all 25 surviving froglets continue to grow regardless of the presence or absence of pelvic girdle abnormalities. On 6.xii.1988, the largest froglet had a snout-vent length of 37 mm and had developed nuptial pads.

The life history pattern of the hybrid conforms to the pattern of Australian hylids⁶.

The larval life span of 51–56 days is in agreement with the 41 days recorded for *L. chloris*³ and 58 days for *L. infrasfrenata*⁷ considered usual among tropical species adapted to life in ephemeral waters⁵.

More importantly, development of a lateral curvature of the tail in larvae at four weeks manifesting as pelvic girdle abnormalities in newly metamorphosed froglets supports the premise of genetic differentiation attained by *L. xanthomera* and its recognition as a separate taxon from *L. chloris*². The development of some apparently normal froglets suggests that these species are closely related.

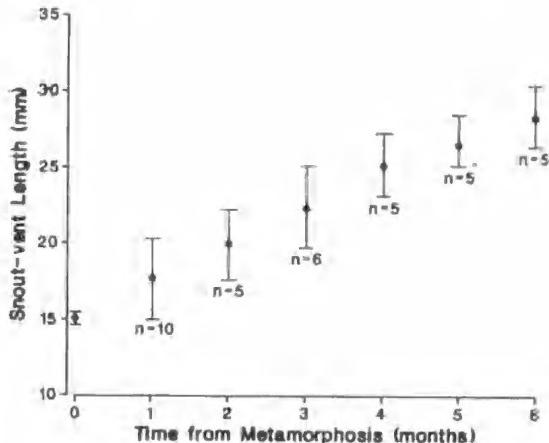


Fig. 5. Growth rate of hybrid offspring from a cross between *Litoria chloris* and *L. xanthomera*. (Mean and range; n = sample size).

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